

# **For Reference**

---

**NOT TO BE TAKEN FROM THIS ROOM**

Ex libris  
UNIVERSITATIS  
ALBERTAENSIS











THE UNIVERSITY OF ALBERTA

MINERAL NUTRITION AND PRIMARY PRODUCTION  
IN NATIVE TUNDRA COMMUNITIES OF THE  
MACKENZIE DELTA REGION, N.W.T.

by



RICHARD WAYNE HAAG

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH  
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE  
OF MASTER OF SCIENCE

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

SPRING, 1972





THE UNIVERSITY OF ALBERTA  
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Mineral Nutrition and Primary Production in Native Tundra Communities of the Mackenzie Delta Region, N.W.T.", submitted by Richard Wayne Haag in partial fulfilment of the requirements for the degree of Master of Science.



## ABSTRACT

Nitrogen and phosphorus nutrition were investigated as limiting factors to primary production in mineral fertilization experiments in two tundra communities, a mesic dwarf shrub-heath, and a wet sedge meadow. Supplementary nutritional studies were carried out under controlled conditions in the laboratory.

Although a high resistance to water uptake due to low soil temperatures was observed in the field with species in both communities, tissue analyses showed that neither nitrogen nor phosphorus uptake were thereby inhibited.

Directly or indirectly, however, low soil temperature, acting on various components of the ecosystem, exerts a major influence on plant production. Response to nitrogen fertilization in both communities, including both increased protein content and dry weight, indicates that the limitation of production by soil nitrogen is not the effect of low temperature acting on the plant. Nitrogen, if available, can be taken up and metabolized into functional organic compounds. The quantity of available soil nitrogen however, is kept at a low level by low temperature inhibition of microbial decomposition and nitrogen cycling.

Lack of response to phosphorus fertilization indicates that available soil phosphorus is not quantitatively limiting to production. Phosphorus metabolism may be direct-



## ABSTRACT (CONTINUED)

ly limited by low soil temperature, or, as the increased response to nitrogen and phosphorus vs. nitrogen fertilization shows, by low levels of available soil nitrogen.

The importance of a low nutrient regime in the Arctic may be seen in the widespread occurrence of xeromorphic characters in many taxa, which thereby require only minimal mineral nutrition to best utilize their photosynthetic capacity. The low nutrient regime may also serve as a partial explanation for the high proportion of perennial species in the Arctic, since these species are able to accumulate a nutrient pool from a deficient environment over time.



## ACKNOWLEDGEMENTS

I wish to extend my thanks to a number of people who have offered their help during the course of this study.

Mr. Alan Godkin provided able assistance and welcome companionship in the field during the summer of 1971.

Mr. Tom Peters, of the Alberta Soil Survey, arranged for shipping and receipt of soil and plant samples. Analyses were carried out at the Department of Agriculture Soil and Feed Testing Laboratory in Edmonton, under the supervision of Mr. Jim Carson.

Dr. Paul R. Gorham provided spectrophotometric equipment for use in plant pigment analyses.

Drs. James Mayo and Steve Pawluk provided valuable guidance and criticism during the development of the research and preparation of the manuscript.

Particular thanks are given to Drs. Lawrence Bliss and Ross Wein, who have offered constant advice and assistance from the beginning, both in the field and back home, and have helped greatly in the preparation of the manuscript. Their concern and guidance has been appreciated.

Imperial Oil Canada, Ltd., provided both transportation and generous accomodation in the field.

Additional financial and logistic support was provided by the Inuvik Research Laboratory, the Arctic Land Use Research Program of DIAND, and the Arctic Petroleum Operator's Association. The University of Alberta provided a Graduate Teaching Assistantship for 1970-71 and 1971-72.





## TABLE OF CONTENTS

|                                   | Page |
|-----------------------------------|------|
| INTRODUCTION                      | 1    |
| REVIEW OF THE LITERATURE          | 3    |
| METHODS                           | 8    |
| RESULTS                           | 15   |
| Plant Communities and Soils       | 15   |
| Dwarf shrub-heath Community       | 15   |
| Wet Sedge Meadow Community        | 18   |
| Plant and Soil Water Potentials   | 19   |
| Dwarf shrub-heath Community       | 19   |
| Wet Sedge Meadow Community        | 21   |
| Plant and Soil Mineral Nutrition  | 24   |
| Dwarf shrub-heath Community       | 24   |
| Soil Nutrient Status              | 24   |
| Community and Species Production  | 29   |
| Physiological Response            | 33   |
| Nutrient-Temperature Interactions | 38   |
| Wet Sedge Meadow Community        | 47   |
| Soil Nutrient Status              | 47   |
| Community Production              | 50   |
| Physiological Response            | 52   |
| DISCUSSION                        | 61   |



## TABLE OF CONTENTS (continued)

|                  | Page |
|------------------|------|
| CONCLUSIONS      | 75   |
| LITERATURE CITED | 79   |



# LIST OF TABLES

| Table |                                                                                                                                                           | Page   |
|-------|-----------------------------------------------------------------------------------------------------------------------------------------------------------|--------|
| 1     | Cover and frequency values for a dwarf shrub-heath community near Tuktoyaktuk, N.W.T.                                                                     | 16     |
| 2     | Profile description of an Orthic Gleysol developed under a dwarf shrub-heath community near Tuktoyaktuk, N.W.T.                                           | 17     |
| 3     | Frequency values for a wet sedge meadow community near Tuktoyaktuk, N.W.T.                                                                                | 18     |
| 4     | Results of chemical analyses of an Orthic Gleysol near Tuktoyaktuk, N.W.T.                                                                                | 26, 27 |
| 5     | Dry weight above ground production ( $\text{g/m}^2$ ) in a dwarf shrub-heath community near Tuktoyaktuk, N.W.T.                                           | 30, 31 |
| 6     | Results of chemical analyses of <u>Betula nana</u> current leaves; dwarf shrub-heath community near Tuktoyaktuk, N.W.T.                                   | 34, 35 |
| 7     | Fresh and dry weight production (g) over 10 weeks of <u>Lupinus arcticus</u> in relation to temperature and nitrogen nutrition.                           | 42     |
| 8     | Absorbance of chlorophyll extracts of equivalent weight samples of <u>Lupinus arcticus</u> leaf tissue in relation to temperature and nitrogen nutrition. | 42     |
| 9     | Absorbance of flavonoid extracts of equivalent weight samples of <u>Lupinus arcticus</u> leaf tissue in relation to temperature and nitrogen nutrition.   | 44     |
| 10    | Results of chemical analyses of organic soil from a wet sedge meadow community near Tuktoyaktuk, N.W.T.                                                   | 48, 49 |
| 11    | Total above ground dry weight production in a wet sedge meadow community near Tuktoyaktuk, N.W.T.                                                         | 51     |
| 12    | Results of chemical analyses on total production material from a wet sedge meadow community near Tuktoyaktuk, N.W.T.                                      | 53, 54 |



## LIST OF TABLES (continued)

| Table |                                                                                                                        | Page |
|-------|------------------------------------------------------------------------------------------------------------------------|------|
| 13    | Estimated annual organic matter decomposition in two tundra communities near Tuktoyaktuk, N.W.T.                       | 64   |
| 14    | Estimated annual nutrient release from organic matter decomposition in two tundra communities near Tuktoyaktuk, N.W.T. | 67   |





## LIST OF FIGURES

| Figure |                                                                                                                    | Page |
|--------|--------------------------------------------------------------------------------------------------------------------|------|
| 1a     | Seasonal variation in soil water potential at 5 cm depth in a dwarf shrub-heath community near Tuktoyaktuk, N.W.T. | 20   |
| 1b     | Seasonal variation in <u>Betula nana</u> ssp. <u>exilis</u> leaf water potential.                                  | 20   |
| 1c     | Seasonal variation in <u>Vaccinium vitis-idaea</u> ssp. <u>minus</u> leaf water potential.                         | 20   |
| 2      | Seasonal variation in soil and air temperature profiles in a dwarf shrub-heath community near Tuktoyaktuk, N.W.T.  | 22   |
| 3a     | Diurnal variation in soil water potential at 5 cm depth in a dwarf shrub-heath community near Tuktoyaktuk, N.W.T.  | 23   |
| 3b     | Diurnal variation in soil temperature profiles in a dwarf shrub-heath community near Tuktoyaktuk, N.W.T.           | 23   |
| 4a     | Seasonal variation in <u>Carex rariflora</u> leaf water potential.                                                 | 25   |
| 4b     | Seasonal variation in <u>Eriophorum russeolum</u> leaf water potential.                                            | 25   |
| 5a     | <u>Lupinus arcticus</u> shoot growth at 15°C and varying nitrogen levels.                                          | 39   |
| 5b     | <u>Lupinus arcticus</u> shoot growth at 5°C and varying nitrogen levels.                                           | 39   |
| 6a     | <u>Lupinus arcticus</u> root growth at 15°C and varying nitrogen levels.                                           | 40   |
| 6b     | <u>Lupinus arcticus</u> root growth at 5°C and varying nitrogen levels.                                            | 40   |



## LIST OF FIGURES (continued)

| Figure |                                                                                                                                        | Page |
|--------|----------------------------------------------------------------------------------------------------------------------------------------|------|
| 7      | Seasonal variation in air and soil temperature profiles in a wet sedge meadow community near Tuktoyaktuk, N.W.T.                       | 55   |
| 8      | Compartment model showing the interactions between environmental factors and plant metabolism in the limitation of primary production. | 62   |



## INTRODUCTION

One of the definitive characteristics of arctic tundra ecosystems is that, relative to temperate ones, the vegetation exhibits a low amount of net annual production. The nature of factors responsible for this are of importance in understanding the functioning of natural ecosystems and the adaptations of organisms to their environment.

In recent years, the low rate of biomass accumulation has become of more than academic interest, since this renders tundra ecosystems more sensitive to alteration of natural conditions, and decreases the rate of recovery following disturbance, relative to our experience in more temperate regions.

A number of causal factors have been postulated for this low rate of primary production, among them: low availability of soil water, the mineral nutrient status of tundra soils, and low air and soil temperatures, the latter due to the occurrence of permafrost underlying a shallow active layer throughout the Arctic. These factors are also of interest in that they may be affected by the activities of man.

The present study was carried out with a twofold objective: first, to determine specific cause-effect relations limiting production in tundra communities from the results of field and laboratory experiments, and second, to develop a generalized concept regarding these limitations in rela-



tion to structural and functional adaptations of arctic ecosystems.

Nomenclature for vascular plants follows Hultén (1968), with the exception of Salix pseudopolaris, which follows Porsild (1964). Voucher specimens have been deposited with the University of Alberta Herbarium, and with the Jesup Herbarium of Dartmouth College.





## REVIEW OF THE LITERATURE

Limitation of photosynthesis and carbohydrate production by low air temperature in the Arctic is perhaps the first factor which occurs to people. Warren-Wilson (1957), among others, has shown that air temperatures are not, in fact, extremely low. The low growth habit of many species constitutes an effective adaptation to the arctic energy regime. Temperatures within the boundary layer rise well above ambient, creating a microenvironment favorable to plant growth (Warren-Wilson, 1957; Courtin, 1968).

Other plant species, notably the graminoids, lack such a well developed individual boundary layer, and thus may be more closely tied to ambient conditions (Courtin, 1968). In meadow communities, however, the community boundary layer may serve the same function for these species as the individual boundary layer in low growing ones.

Low water availability has been implicated as a limiting factor in a number of ways. In many areas of the High Arctic, it may be that the amount of water, often expressed as a percent of dry soil, is quite low, which may be a factor in the existence of polar desert. These areas receive low annual precipitation, mainly in the form of snow. Yearly soil temperatures are low, and wind velocities high, and much of the water may never enter the soil. In the Mackenzie Delta region, however, this factor appears to be of little importance.



The concept of physiological aridity has been put forward by a number of workers. Decreased thermal energy directly lowers soil water potential, and Sorenson (1941) has stated that root competition for water due to low soil temperatures is an important factor limiting plant growth in the Arctic. Firbas (1931), however, has shown that water uptake by Eriophorum vaginatum is scarcely affected by lowered soil temperature, but this question has not received adequate experimental investigation.

Soil pH has also been postulated as a possible cause of physiological aridity. Saebø (1968) has suggested that high amounts of organic acids in peats may inhibit water uptake, and this could be an important factor in much of the Arctic where peats predominate.

Mineral nutrition as a limiting factor has received intensive investigation by a number of workers. Russell (1940), studying the development of vegetation on Jan Mayen Island, found a significant increase in plant cover correlated with the presence of animal droppings, and concluded that a low supply of available soil nitrogen was important in the limitation of production. In addition, he hypothesised an effect of phosphorus availability, but did not demonstrate this. He related available nitrogen supply to both microbial activity and increased plant cover, and thus as a limiting mechanism his argument becomes somewhat circular. Warren-Wilson (1954, 1959) also reported an increase



in plant cover under the same conditions. These findings have been concerned primarily with empirical evidence, however, and not with how such a nutrient limitation might arise or limit production physiologically.

Mineral nutrition has been studied extensively from an autecological point of view, particularly in bogs in Northern Europe (Tamm, 1954; Miller, 1963; Saebø, 1968, 1969, 1970), and in England (Gore, 1961a, b, 1963). Results have varied with both the species and the geographical area studied, preventing the formulation of any sound general conclusions. Results of fertilization experiments have likewise been variable.

Miller (1963) demonstrated a general effect of mineral nutrition on the development and phenotype of plants in far northern bogs. He suggested that the nitrogen regime might be the cause of xeromorphy common to plants in these areas. Saebø (1968) reported that limitation by phosphorus may be an additional important factor in these bogs.

The role of soil temperature as a limiting factor has received a great deal of attention, particularly in relation to the physiology of mineral nutrition. Blackman (1936) demonstrated inhibition of nitrogen uptake by low spring soil temperatures in pasture grasses. The Soviet workers have addressed themselves to this question extensively, but much of this work was carried out during the Virgin Lands Program in the late 1950's, and for this reason deals chief-





ly with agronomic species (Dadykin, 1958).

Dadykin (1958) demonstrated a large decrease in nitrogen uptake by plants grown at low soil temperatures ( $3^{\circ}\text{C}$ ), and a much smaller decrease at  $6-7^{\circ}\text{C}$ . Nitrogen metabolism was shown to be strongly affected by low soil temperatures as well. Wheat synthesises only 4 amino acids at  $6-7^{\circ}\text{C}$ , and potato loses the ability to synthesise 3 complex amino acids (phenylalanine, tyrosine, and proline) (Dadykin, 1958). Protein content of plants grown at low temperatures falls off sharply as well.

Phosphorus uptake and metabolism at low temperatures have likewise been studied. In oats, rye, and potatoes, total phosphorus content of the plant is sharply decreased by a drop in soil temperature from  $20^{\circ}\text{C}$  to  $6^{\circ}\text{C}$ , while nitrate content of above ground parts seems less strongly affected (Zhurbitsky and Shtrausberg, 1954, 1958; Shtrausberg, 1958). Korovin has likewise demonstrated a 50% decrease in total phosphorus content at  $6^{\circ}\text{C}$ , and a major effect on metabolism as well (Korovin et al., 1963). Phosphorus incorporation, particularly into nucleoproteins, appears strongly inhibited by low temperatures in potatoes and wheat, which results in a decreased protein content. In field experiments, a doubling of phosphorus in NPK fertilizer applied to permafrost soils brought about a 73% increase in shoot dry weight production in potatoes, and a 135% increase in tuber dry weight production.





Under low temperatures, total P increased, but the bulk remained in inorganic form, with only leaf nucleoproteins showing an increase (Korovin et al., 1963). Protein content increased slightly. Under a higher temperature regime, total P did not appear to be affected, but organic P increased.

These results demonstrate a major effect of both mineral nutrition and soil temperature on secondary metabolism and production, and suggest a possible interaction between nitrogen and phosphorus in the limitation of production. These results have been demonstrated primarily with agronomic species, which have evolved in temperate regions under the influence of man's selection. We thus cannot yet safely apply these results to native arctic species and communities, since these have evolved under different environmental conditions, and may have developed differing physiological responses.



## METHODS

Five weeks during the summer of 1970 were spent in orientation and a general survey of the Mackenzie Delta Region, to determine major soil and vegetation types and their extent. It was decided to concentrate on the effect of mineral nutrition and temperature on primary production. Water availability was, additionally, measured during the course of this study, primarily in relation to nutrient uptake.

Based on this survey work, an intensive study site was established in May, 1971, on the Tuktoyaktuk Peninsula, approximately 2 km south of the Imperial Oil Base Camp. Two representative communities were chosen for study: a wet sedge meadow, consisting primarily of Carex rariflora, C. chordorhiza, and Eriophorum russeolum on an organic soil, and a dwarf shrub-heath community, developed on a mineral soil overlain by a 10 cm thick humic horizon, typical of much of the upland tundra of this area. These communities were chosen because of their divergence in physiognomic and environmental characteristics within the geographic area.

Fourteen 5 X 5 m plots, separated by a 1.5 m buffer zone, were established in each community for the investigation of mineral nutrition. Duplicate plots were fertilized at the following rates in kg/ha: control (no treatment),



100N, 100P, 100N + 100P, 200N, 200P, 200N + 200P. Nitrogen was applied as ammonium nitrate (34% N), and phosphorus as  $P_2O_5$  (Superphosphate- 20% P). Nitrogen and phosphorus were chosen for investigation since these are the mineral elements required in largest quantities by plants, and thus most likely to limit production, and on the basis of previous work (Russell, 1940; Warren-Wilson, 1957, 1959). Fertilizers were applied on 29 May, 1971 in the dwarf shrub-heath community, but not until 12 June, 1971 in the wet sedge meadow, since this community was covered with water up until this time.

Thermocouples were implanted in the soil at depths of 5 and 10 cm at 10 sites in each community. Sixteen porous cup chromel/constantan thermocouple psychrometers (Wescor PT-10) were implanted at a depth of 5 cm in the dwarf shrub-heath community to monitor soil water potential through the growing season, but this was not done in the wet sedge meadow, due to the water saturated condition of the soil for most of the growing season. At weekly intervals, temperature profiles and soil water potentials were measured. Leaf water potentials were measured for two species in each community for the first several weeks of the growing season, using a Wescor sample chamber psychrometer. Four determinations were made for each species studied at each nutrition level.

The effect of mineral fertilization on above ground





vascular plant production was determined by the harvest method at three times during the growing season. Ten 20 X 50 cm quadrats were located in a stratified random fashion within each duplicate plot, and the vegetation was clipped to the moss layer, to give a total of 20 samples per treatment in each community. Material was collected in paper bags and dried within 24 hr of collection at 60°C for 24 to 36 hr. Sampling intensity was determined by a preliminary harvest of standing crop, and this sample size was found sufficient to reduce the standard error of standing crop to 15% or less for each of the major species in the dwarf shrub-heath community.

Dry weight of current leaf, twig, and reproductive part growth was used as a measure of production. This results in an underestimate of production (Whittaker, 1963), since radial growth is not accounted for, but this has been found to be low in tundra regions (Bliss, 1970) and results for the different treatments are comparable. Production was separated by species in the dwarf shrub-heath, but this was not done in the wet sedge meadow, due to uncertainty of identification of vegetative plants. Means and standard errors for dry weight production were calculated, and the results analysed by the random block analysis of variance (Snedecor, 1957). Duncan's Multiple Range Test (Duncan, 1965) was used to test the significance of mean differences.

A random sample from each treatment of dried current





leaf production of Betula nana, and of total leaf production from the wet sedge meadow, was analysed for total protein, nitrate, fiber, phosphorus, calcium, and potassium contents (Horwitz, 1970).

A second portion of Betula nana leaf material was retained for pigment analysis. Total flavonoids, including anthocyanins, flavones, and flavonols, were initially extracted from 0.1 g dry ground leaf samples in 5 ml hot methanol for 2 minutes. This undoubtedly resulted in the breakdown of anthocyanins to anthocyanidins (Harborne, 1967) but this was not important since interest centered on the relative concentration of parent 15 carbon skeletons, and not on the qualitative identification of individual compounds. Tissue was then ground with an additional 5 ml methanol, and washed through a sintered glass filter with a final 10 ml. Relative total flavonoid content was determined from the ultraviolet 220-440 nm scan of an aliquot of this sample diluted appropriately, using a Beckman DB-G grating spectrophotometer with hydrogen lamp source, in matched quartz cells. Duplicate extractions and determinations were run for each treatment. Relative total flavonoid content of field samples of Betula nana leaves is reported as the sum of absorbances at 271, 281s, 330, and 355 nm. These were the only peaks observed in the UV range for this species.

At the time of each harvest, two soil cores were taken



from each plot and pooled for nutrient analysis, to give duplicate samples per treatment. In the dwarf shrub-heath, cores were divided by horizon, while in the wet sedge meadow, they were divided into 10 cm segments. These samples were dried in the air for 24 hr, and frozen within 48 hr of collection at  $-30^{\circ}\text{C}$ . This treatment undoubtedly drove off some available nitrogen, but was necessitated by the moist, highly organic nature of the soils. Samples were later dried in the laboratory at  $60^{\circ}\text{C}$ , and analysed for available phosphorus, potassium, and calcium, total nitrogen, sulfate, pH, and conductivity (Horwitz, 1970). Total exchange capacity was determined by ammonium acetate leaching (Horwitz, 1970).

Organic matter was determined from loss on ignition at  $450^{\circ}\text{C}$  for 1 hr. Bulk density was determined from known volume cores.

At the time of peak production and flowering, determinations of vegetation composition and soil type were made in each community. In the dwarf shrub-heath, cover and frequency values by species were determined from 140 randomly located quadrats during the second harvest prior to clipping. Two soil pits were dug, and the soil described according to the Canadian system (Canada Dept. Agriculture, 1970). Soil pH was determined by horizon with a Truog Soil Testing Kit, and color according to Munsell Notation.

In the wet sedge meadow, only frequency was determined



in the 140 20 X 50 cm quadrat samples. A single soil pit was dug, and pH determined, but extensive description of this soil was not attempted.

Some aspects of the limitation of production by temperature, as well as the physiology of mineral nutrition, were investigated in growth chamber experiments at the University of Alberta.

The interaction of mineral nutrition and temperature was studied with Lupinus arcticus, a legume common in the dwarf shrub-heath, and easily grown from seed.

One hundred plants were grown from seed on moistened filter paper in Petri dishes. Thirty six 10 day old seedlings were then chosen randomly, placed in 21 polyethylene hydroponic culture vessels, and grown in standard Hoagland's solution (Hoagland and Arnon, 1938), in which nitrate nitrogen levels were adjusted to 0.01, 0.007, and 0.003 M. pH was adjusted to 5.5 with 0.1 M HCl or NaOH. Six plants were grown at each nutrition level at both 5' and 15°C, under constant light and 70% relative humidity, for 10 weeks. Nutrient solutions were changed weekly, and at the time of solution change, each plant was measured for both total root and stem elongation.

At the end of the experimental period, plants were removed from solution, rinsed in distilled water, blotted dry, and cut into root and stem portions. Fresh weight production was determined, and one half the plants from each treat-





ment were dried at 60<sup>o</sup>C for 24 hr, to permit conversion to dry weight production, and to preserve flavonoid compounds in an unaltered form (Geisman, 1955). Flavonoid content was determined with dried, ground 0.05 g Lupinus leaf samples by the aforementioned method. Relative total flavonoid content of Lupinus arcticus leaves is reported as the sum of absorbances at 262 and 337 nm. Each value is the mean of three determinations.

Fresh samples were used to determine the effect of temperature and nitrogen nutrition on chlorophyll content. Total chlorophyll was extracted in 10 ml hot ethanol per g fresh weight of tissue. Chlorophyll content was determined from the absorbances of an appropriate dilution of an aliquot of this extract at the following wavelengths: chlorophyll a- 445 and 665 nm, and chlorophyll b- 470 and 615 nm. These peaks were determined from the spectral scan of the same samples on a Beckman DB-G grating spectrophotometer. Relative chlorophyll content is reported as the sum of absorbances at these four wavelengths, and each value is the mean of three determinations.





## RESULTS

### Plant Communities and Soils

#### Dwarf shrub-heath Community

Cover and frequency values for the dwarf shrub-heath community are presented in Table 1. The discontinuous low shrubby layer is composed primarily of Betula nana ssp. exilis, with a lesser amount of Salix glauca. Major ground cover of prostrate vascular plants is more continuous, and is composed primarily of Vaccinium vitis-idaea ssp. minus, Ledum palustre var. decumbens, and Empetrum nigrum ssp. hermaphroditum. This community fits the description of the dwarf shrub-heath type of Churchill (1955) in Alaska, based on species of highest frequency. The high frequency of Carex bigelowii places this in the Betula-Carex subtype, a dry phase of the dwarf shrub-heath.

This community is developed on a soil consisting of a dark, moderately thick humus layer averaging 10 cm in thickness, overlying a thin, discontinuous, but structurally well developed Bg horizon. Both the Bg and Czg horizons show strong gleying, evidenced in prominent mottles and low chromas, indicating a high but fluctuating water content during the growing season (Table 2). The soil is developed from reworked glacial till (MacKay, 1963), and on the basis of physical and chemical characteristics has been classified as an Orthic Gleysol under the Canadian system.



Table 1. Cover and frequency values for a dwarf shrub-heath community near Tuktoyaktuk, N.W.T.

| Species                                           | Frequency (%) | Cover (%) |
|---------------------------------------------------|---------------|-----------|
| <u>Vaccinium vitis-idaea</u> ssp. <u>minus</u>    | 98            | 18.98     |
| <u>Empetrum nigrum</u> ssp. <u>hermaphroditum</u> | 93            | 13.80     |
| <u>Betula nana</u> ssp. <u>exilis</u>             | 86            | 14.13     |
| <u>Ledum palustre</u> var. <u>decumbens</u>       | 89            | 8.12      |
| <u>Carex bigelowii</u>                            | 90            | 4.72      |
| <u>Salix glauca</u>                               | 54            | 8.34      |
| <u>Vaccinium uliginosum</u>                       | 19            | 1.0       |
| <u>Pyrola grandiflora</u>                         | 51            | <1        |
| <u>Lupinus arcticus</u>                           | 21            | <1        |
| <u>Pedicularis Kanei</u> ssp. <u>Kanei</u>        | 14            | <1        |
| <u>Hierochloë alpina</u>                          | 12            | <1        |
| <u>Pyrola secunda</u>                             | 4             | <1        |
| <u>Pedicularis capitata</u>                       | 2             | <1        |
| <u>Saussurea angustifolia</u>                     | 2             | <1        |
| <u>Senecio atropurpurea</u>                       | 1             | <1        |
| <u>Arctostaphylos rubra</u>                       | 1             | <1        |
| Mosses                                            | 96            | 16.1      |



Table 2. Profile description of an Orthic Gleysol developed under a dwarf shrub-heath community near Tuktoyaktuk, N.W.T.

| Horizon         | Depth(cm) | Color                   | Texture            | Mottles                         | Structure                         | Consistence        | pH      |
|-----------------|-----------|-------------------------|--------------------|---------------------------------|-----------------------------------|--------------------|---------|
| L-F             | 3-15      | 10R 2/2m                | --                 | --                              | --                                | --                 | 5.0-5.5 |
| H               | 5-20      | 5YR 2/1m                | peat-loam          | --                              | --                                | --                 | 5.5-6.0 |
| Bg <sup>1</sup> | 4-35      | 2.5Y 3/2m<br>1.25Y 5/2d | clay-<br>clay-loam | many, fine<br>distinct<br>brown | fine-med,<br>med-str.<br>granular | firm               | 6.5-7.0 |
| Czg             | 20-35+    | 5Y 4/1m                 | clay               | "                               | massive                           | sticky,<br>plastic | 6.5-7.5 |

<sup>1</sup> % base saturation (Ca, Mg, Na, K) of the Bg horizon was 95.5%, exclusive of ammonium.

Developed on a poorly drained site from reworked glacial till. Maximum depth of the active layer 40-45 cm.



Similar soils have been described as a mesic phase of a drainage catena from Alaska as upland tundra soil (Tedrow and Cantlon, 1958).

### Wet Sedge Meadow Community

Frequency values from the wet sedge meadow show Carex rariflora and C. chordorhiza to be the major species, with Eriophorum russeolum an important component (Table 3).

Table 3. Frequency values for a wet sedge meadow community near Tuktoyaktuk, N.W.T.

| Species                         | Frequency (%) |
|---------------------------------|---------------|
| <u>Carex rariflora</u>          | 92            |
| <u>Carex chordorhiza</u>        | 64            |
| <u>Eriophorum russeolum</u>     | 55            |
| <u>Eriophorum angustifolium</u> | 12            |
| <u>Carex membranacea</u>        | 9             |
| <u>Salix pseudopolaris</u>      | 3             |
| <u>Andromeda polifolia</u>      | 2             |
| <u>Pedicularis sudetica</u>     | <1            |
| <u>Potentilla palustris</u>     | <1            |

The vegetation is thus similar to the water soaked ground swamp described by Seidenfaden and Sorenson (1937) in Greenland. Frequent and less important species place this in Hanson's (1951, 1953) sequence of lowland hummock and hollow communities, while the relative absence of microre-





lief places this as a wet phase of Hanson's sequence.

The wet sedge meadow community is discontinuous within a series of low center polygons, and comprises part of a complex mosaic of communities. Within the polygons, vegetation is highly homogeneous, and is developed on an organic soil extending beyond the maximum active layer depth. The soil is a moderately well decomposed Carex peat, with a low pH of approximately 5.4, and a relatively high total exchange capacity (75.6 meq/100 g soil). The active layer is shallow throughout the growing season, due to the insulating effect of the water soaked peat.

#### Plant and Soil Water Potentials

##### Dwarf shrub-heath Community

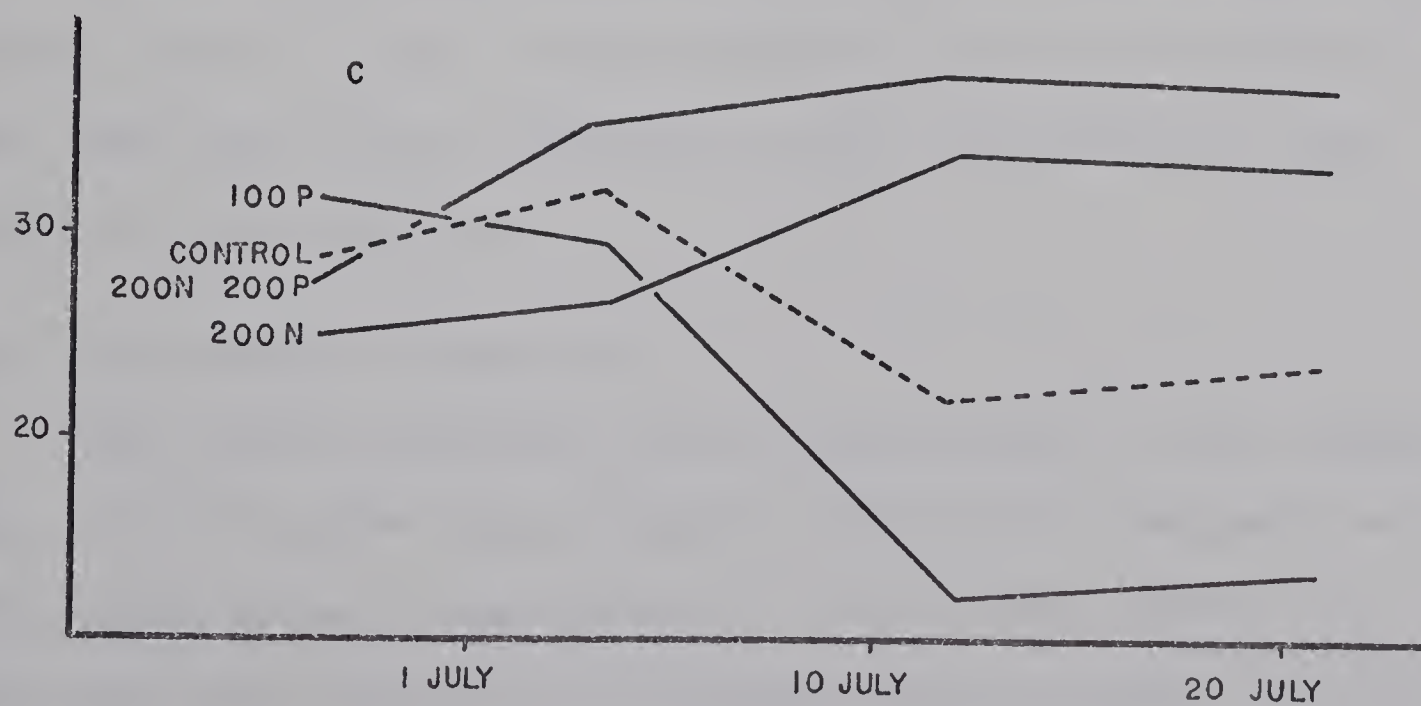
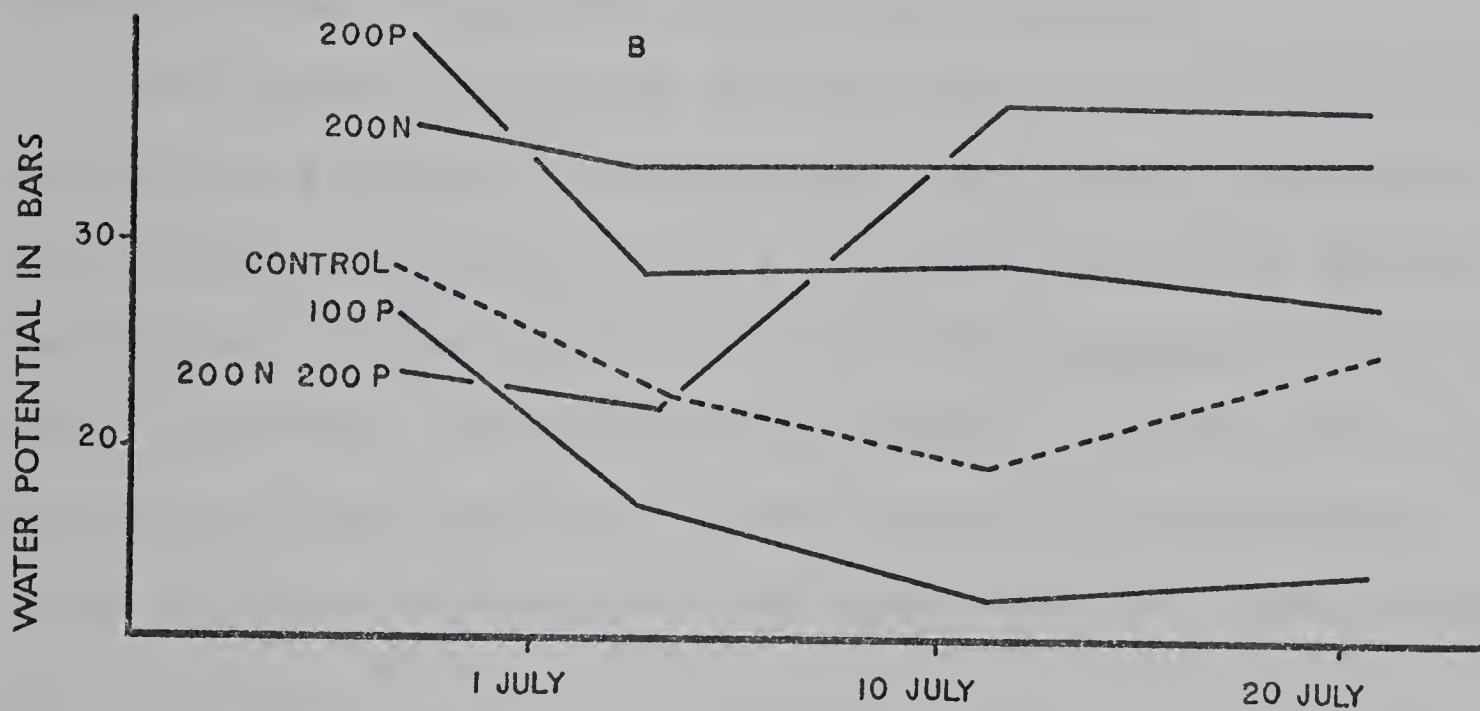
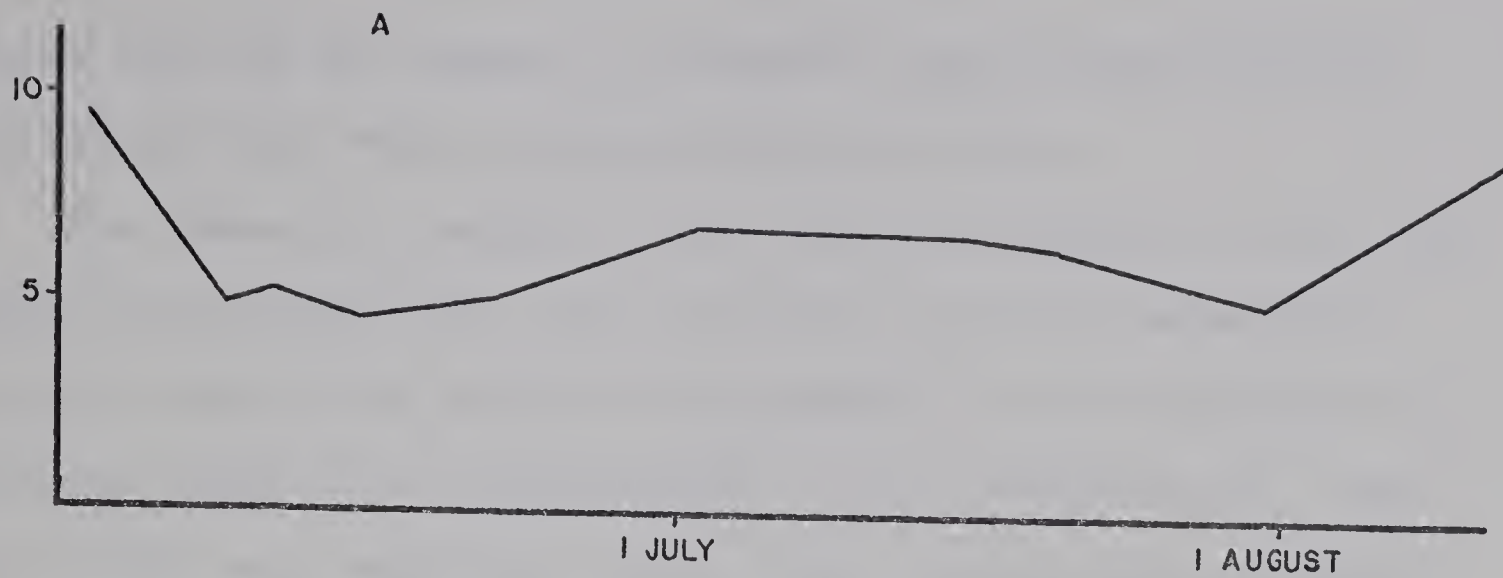
The values for soil water potential within the H horizon of maximum rooting average -6 to -7 bars throughout the growing season (Fig. 1a). Leaf water potentials of Betula nana and Vaccinium vitis-idaea control plants average from -20 to -25 bars (Fig. 1b, c).

Water potential gradients (soil to leaf) are thus relatively steep, indicating a high resistance to water movement from the soil into the plant. The resistance to water movement may be due to a number of factors, including decreased permeability of cells, increased viscosity of protoplasm, and increased viscosity of water, all of which are directly related to low soil temperature (Kramer, 1949), and have been observed for temperate species (Kramer, 1934, 1940). Tundra

Figure 1a. Seasonal variation in soil water potential at 5 cm depth in a dwarf shrub-heath community near Tuktoyaktuk, N.W.T.

Figure 1b. Seasonal variation in Betula nana ssp. exilis leaf water potential.

Figure 1c. Seasonal variation in Vaccinium vitis-idaea ssp. minus leaf water potential.



DATE



plants thus do not appear to possess unique physiological adaptations for water uptake from cold soils.

The seasonal change in soil water potential is not very marked, and comparison with variation in soil temperature (Fig. 2) shows that most of the change in water potential is directly related to fluctuations in soil temperature. Drying of the soil which may occur later in the growing season appears to be compensated for by soil warming.

The diurnal variation in soil water potential can also be seen as a direct consequence of the diurnal variation in soil temperature (Fig. 3a, b). The fact that this diurnal variation in water potential due to the changing thermal regime is as high as the seasonal variation suggests that the concept of physiological aridity due to low soil temperatures may have more validity in areas with less ground cover or soil water.

The low seasonal variation in soil water potential is due at least in part to the absorbent power of the H horizon, and gives some indication of the importance of this layer to the ecosystem.

#### Wet Sedge Meadow Community

Soil water potential was not determined in this community, but from the water soaked condition of the peat, we may assume this to approximate 0. Leaf water potentials from the early part of the growing season average -25 bars

Figure 2. Seasonal variation in soil and air temperature profiles in a dwarf shrub-heath community near Tuktoyaktuk, N.W.T.

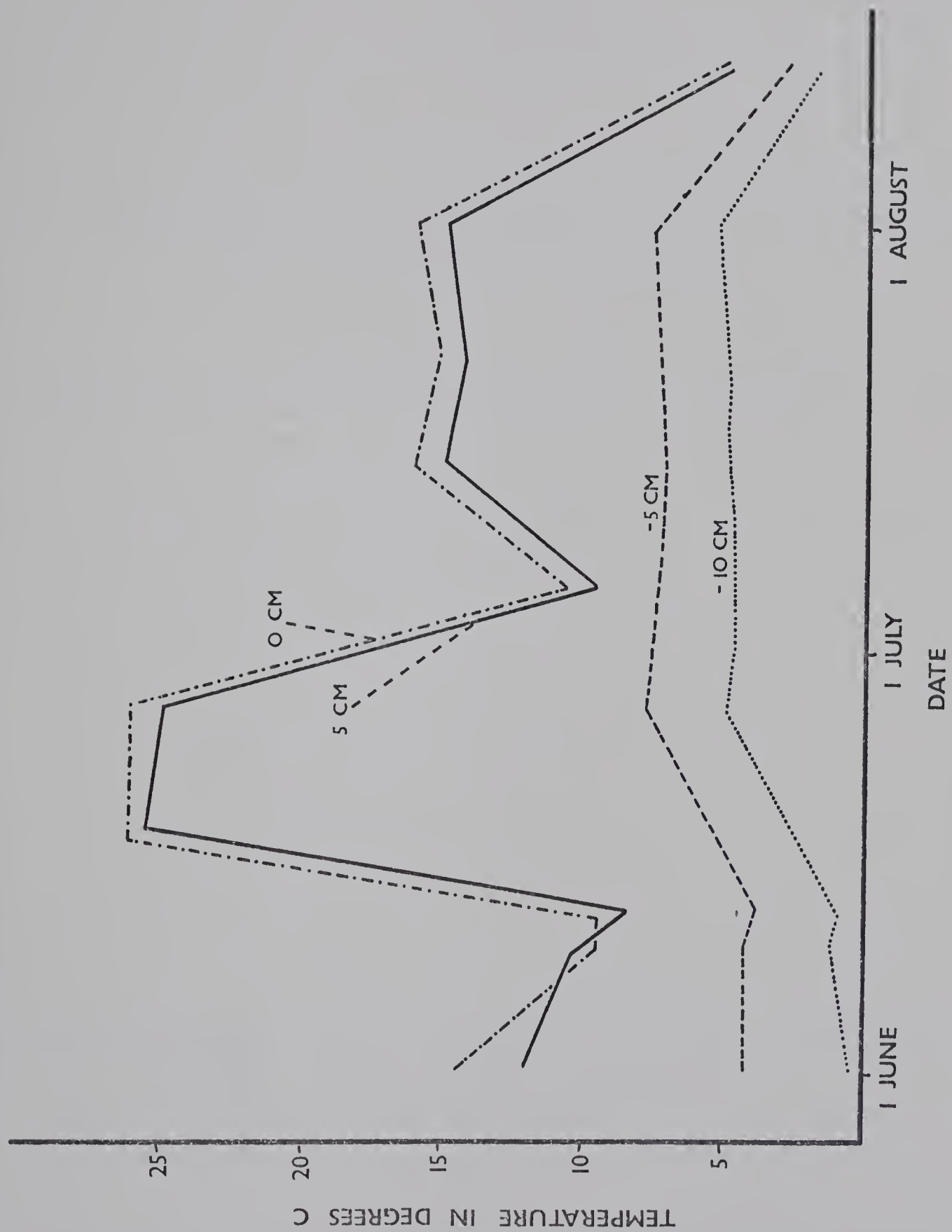
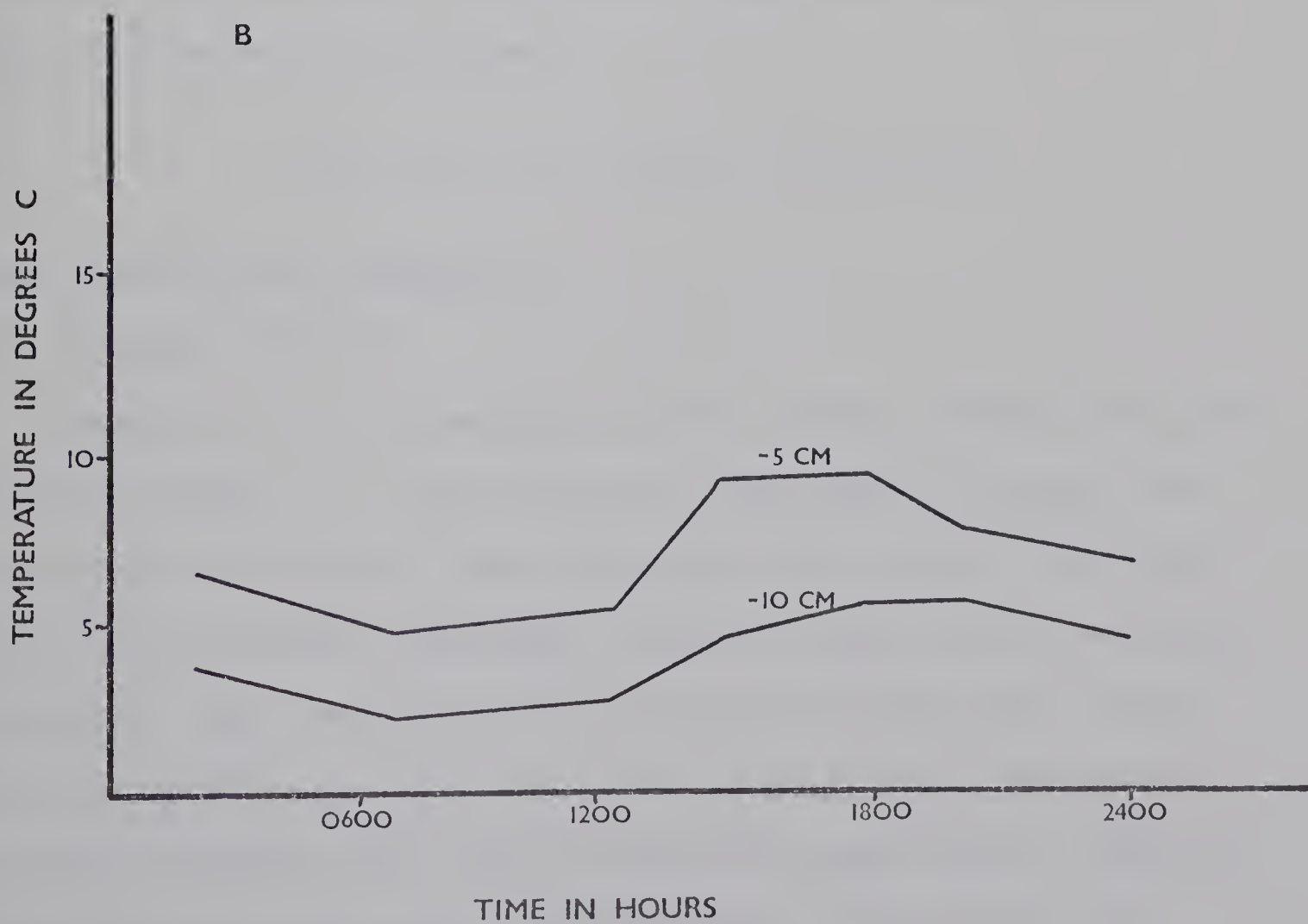
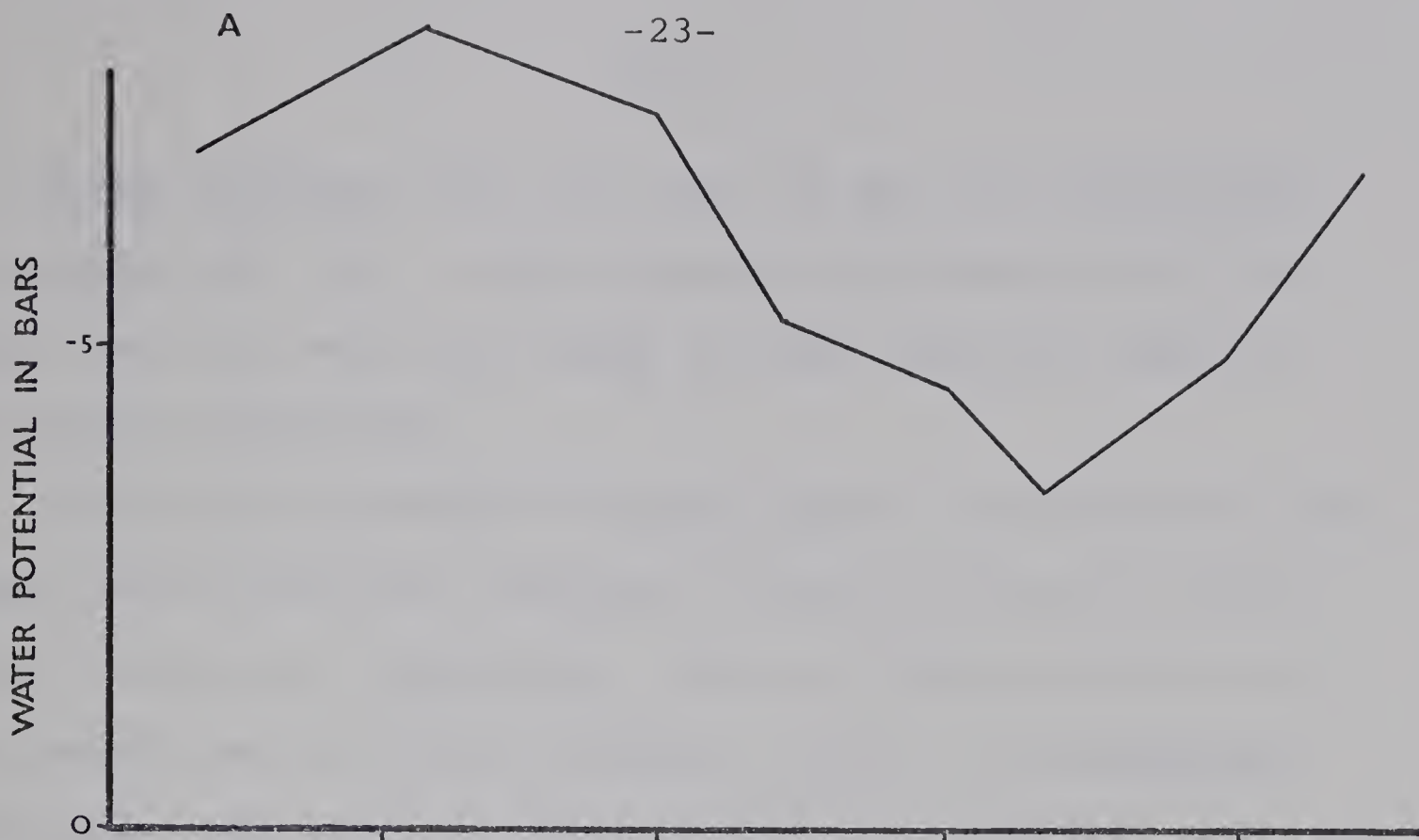


Figure 3a. Diurnal variation in soil water potential at 5 cm depth in a dwarf shrub-heath community near Tuktoyaktuk, N.W.T.

Figure 3b. Diurnal variation in soil temperature profiles in a dwarf shrub-heath community near Tuktoyaktuk, N.W.T.







for Carex rariflora (Fig. 4a) and -35 bars for Eriophorum russeolum (Fig. 4b). Water potential gradients (soil to leaf) are thus even more steep in this community than in the dwarf shrub-heath.

The high resistance to water uptake, accounting for the steep water potential gradient, is again primarily the result of low soil temperature. This is demonstrated by the extremely low leaf water potential values for Eriophorum russeolum, the roots of which extend to permafrost, and are thus exposed to extremely cold soil, in contrast to the dwarf shrub-heath species, in which rooting is generally confined to the upper soil layers, and leaf water potentials are relatively higher.

#### Plant and Soil Mineral Nutrition

##### Dwarf shrub-heath Community

##### Soil Nutrient Status

Results of soil analyses on the Orthic Gleysol are presented in Table 4. The values for available nitrogen are probably considerably lower than the true values for field soils, and probably represent nitrate rather than available nitrogen. The low values of the control plots are, nevertheless, quite striking, while the high values from treated plots indicate that fertilizer did indeed enter solution and become available for plant growth. Variability in

Figure 4a. Seasonal variation in Carex rariflora leaf water potentials.

Figure 4b. Seasonal variation in Eriophorum russeolum leaf water potentials.

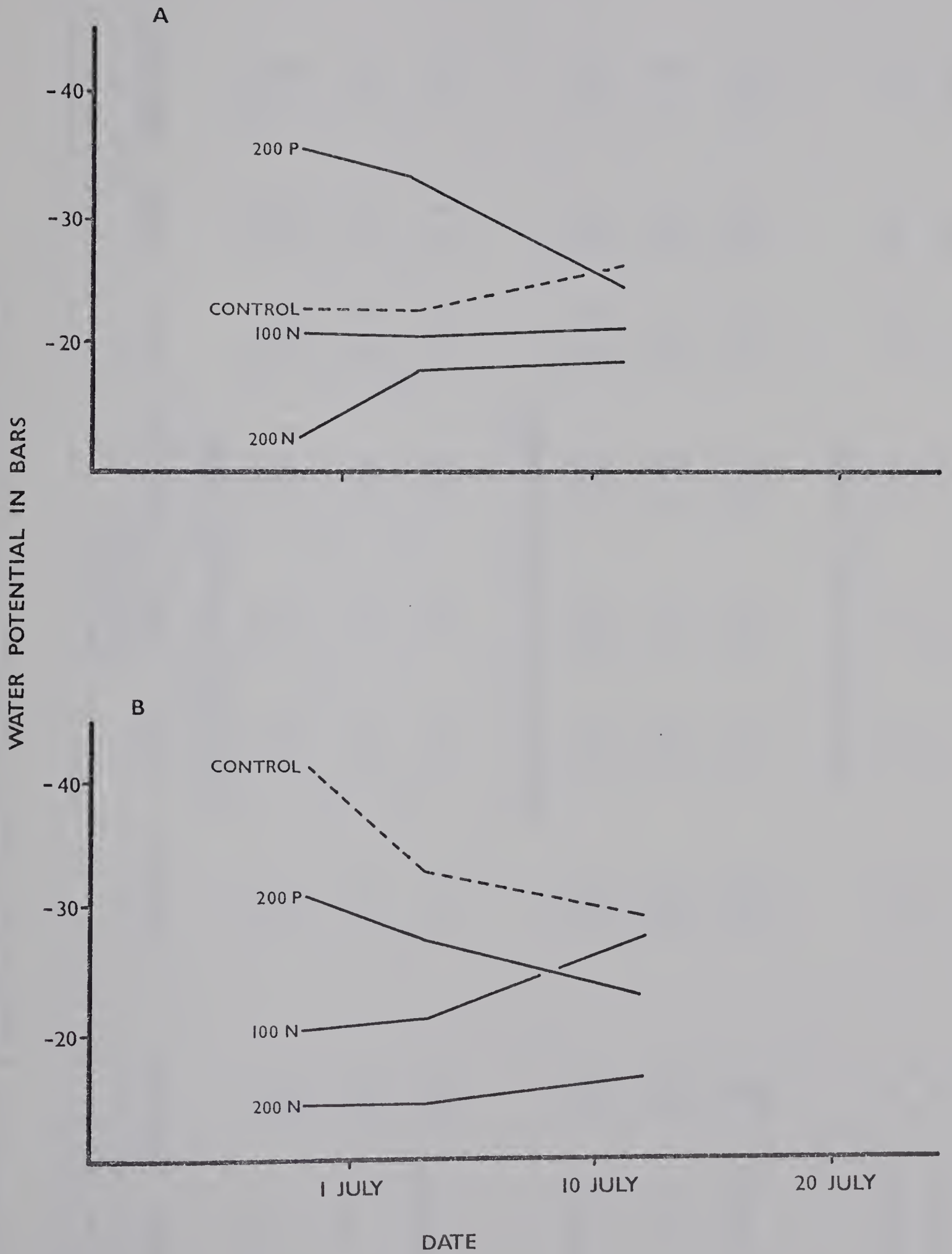




Table 4. Results of chemical analyses of an Orthic Gleysol-  
d warf shrub-heath community near Tuktoyaktuk, N.W.T.

| Date                              | Horizon | Control | Treatment |      |           |      | 200N | 200P | 200N/200P |
|-----------------------------------|---------|---------|-----------|------|-----------|------|------|------|-----------|
|                                   |         |         | 100N      | 100P | 100N/100P | 200N |      |      |           |
| <u>Available Nitrogen (ppm)</u>   |         |         |           |      |           |      |      |      |           |
| 19 June                           | H       | 0.5     | 2.0       | 0.3  | 4.0       | 40.+ | 1.0  | 17.0 |           |
|                                   | B/C     | 0.5     | 0.5       | 0.3  | 0.3       | 0.5  | 0.5  | 0.8  |           |
| 7 July                            | H       | -       | -         | -    | -         | -    | -    | -    |           |
|                                   | B/C     | 1.0     | 0.8       | 0.5  | 0.5       | 0.3  | 0.0  | 0.5  |           |
| 5 August                          | H       | -       | -         | -    | -         | -    | -    | -    |           |
|                                   | B/C     | 0.5     | 0.5       | 0.8  | 0.5       | 1.0  | 0.5  | 0.5  |           |
| <u>Available Phosphorus (ppm)</u> |         |         |           |      |           |      |      |      |           |
| 19 June                           | H       | 11.5    | 4.5       | 26.0 | 13.5      | 8.0  | 36.5 | 23.5 |           |
|                                   | B/C     | 1.0     | 2.0       | 8.5  | 1.0       | 7.0  | 2.0  | 2.0  |           |
| 7 July                            | H       | 8.5     | 8.5       | 17.5 | 20.5      | 6.7  | 49.5 | 66.0 |           |
|                                   | B/C     | 4.7     | 2.0       | 1.0  | 1.0       | 0.7  | 2.0  | 2.2  |           |
| 5 August                          | H       | 7.3     | 9.7       | 90.5 | 22.3      | 7.3  | 36.0 | 41.7 |           |
|                                   | B/C     | 1.0     | 1.5       | 4.5  | 1.3       | 0.3  | 1.5  | 2.5  |           |
| <u>Available Sulfur (ppm)</u>     |         |         |           |      |           |      |      |      |           |
| 19 June                           | H       | 3.9     | 0.6       | 9.2  | 10.1      | 2.6  | 43.1 | 9.9  |           |
| 7 July                            | H       | 7.4     | 8.7       | 21.1 | 6.8       | 5.1  | 20.1 | 21.8 |           |





Table 4. Continued.

| Date     | Horizon | Control | Treatment                 |       |           |       |       |           |  |
|----------|---------|---------|---------------------------|-------|-----------|-------|-------|-----------|--|
|          |         |         | 100N                      | 100P  | 100N/100P | 200N  | 200P  | 200N/200P |  |
|          |         |         | Available Potassium (ppm) |       |           |       |       |           |  |
| 5 June   | H       | 156.5   | 60.5                      | 62.5  | 92.5      | 103.7 | 157.5 | 119.5     |  |
|          | B/C     | 112.5   | 94.0                      | 91.0  | 91.0      | 101.5 | 122.5 | 95.5      |  |
| 7 July   | H       | 159.7   | 148.0                     | 135.0 | 102.3     | 108.3 | 144.0 | 124.5     |  |
|          | B/C     | 116.3   | 110.3                     | 113.3 | 108.3     | 114.0 | 125.0 | 124.0     |  |
| 5 August | H       | 170.5   | 140.3                     | 125.5 | 199.5     | 188.7 | 152.0 | 132.5     |  |
|          | B/C     | 148.5   | 130.3                     | 87.5  | 123.0     | 145.5 | 132.0 | 157.7     |  |
| pH       |         |         |                           |       |           |       |       |           |  |
| 19 June  | H       | 5.65    | 5.00                      | 5.30  | 4.85      | 6.70  | 5.45  | 4.85      |  |
|          | B/C     | 4.80    | 5.15                      | 5.40  | 5.15      | 4.90  | 4.60  | 4.95      |  |
| 7 July   | H       | 5.80    | 5.90                      | 4.90  | 4.60      | 4.90  | 5.40  | 5.85      |  |
|          | B/C     | 5.40    | 5.55                      | 5.30  | 5.45      | 5.90  | 5.75  | 5.35      |  |
| 5 August | H       | 5.70    | 5.30                      | 5.10  | 4.75      | 5.20  | 5.00  | 5.10      |  |
|          | B/C     | 5.90    | 5.80                      | 5.65  | 5.75      | 5.35  | 6.00  | 5.45      |  |



available nitrogen values in treated plots is probably the result of uneven hand scattering during fertilizer application. From the low values in the control plots, we might conclude that the available nitrogen supply is strongly limiting in this community.

The variation in soil pH may help to explain the part played by soil nitrogen in this community. Soil pH values tend to decrease in nitrogen fertilized plots during the growing season (Table 4). This may be the result of stimulation of microbial nitrification by fertilizer application, as mentioned by other workers (Alexander, 1961), resulting in an imbalance in favor of nitrate, and the formation of nitric acid in the soil.

This could also be explained by a preferential uptake of ammonium ions by plants, which would require less energy for transformation into organic form than nitrate, and lead to the same nitrate imbalance in the soil.

The decrease in pH may be responsible for the decrease in available phosphorus relative to the control in the H horizon under 100N and 200N treatments at the first sampling period. The availability of phosphorus is more strongly regulated by chemical, rather than biological factors, in contrast to nitrogen (Alexander, 1961). At low pH, phosphorus tends to form insoluble complexes with iron and aluminum (Overstreet and Dean, 1951), and although iron and aluminum contents were not determined in this soil, the color-



ation and high degree of mottling are evidence for a high iron content.

Results of available phosphorus analyses from this soil are not as striking as in the case of available nitrogen (Table 4). Although fertilizer application did result in a large increase in phosphorus levels, the control has relatively high values, particularly since this element is required by plants in much lower concentrations than nitrogen, in a ratio of approximately 1:10 (Truog, 1951; Sutcliffe, 1962). Thus one might not expect the decrease in available phosphorus with decreased pH to be of major importance for growth and production, or available phosphorus supply to be as strongly limiting as available nitrogen.

Available potassium values from all plots are extremely high, and it appears unlikely that this element is in any way limiting to production.

Values for available sulfur, required in low concentrations relative to both nitrogen and phosphorus, likewise appear to be high and unlikely to be limiting.

#### Community and Species Production

A comparison of total and species production under mineral fertilizer treatment (Table 5) confirms the implications of soil analyses.

Application of nitrogen alone at low and high rates resulted in small total production increases at the first



Table 5. Dry weight above ground production ( $\text{g/m}^2$ ) in a dwarf shrub-heath community near Tuktoyaktuk, N.W.T.

| Date                       | Control               | 100N                   | 100P                  | Treatment             |                        |                       |                        |
|----------------------------|-----------------------|------------------------|-----------------------|-----------------------|------------------------|-----------------------|------------------------|
|                            |                       |                        |                       | 100N/100P             | 200N                   | 200P                  | 200N/200P              |
| Total Production           |                       |                        |                       |                       |                        |                       |                        |
| 5 June                     | 23.7+3.7 <sup>a</sup> | 27.8+4.8 <sup>b</sup>  | 19.8+2.3 <sup>d</sup> | 25.6+3.7 <sup>a</sup> | 28.1+2.7 <sup>b</sup>  | 26.9+3.4 <sup>b</sup> | 32.3+3.8 <sup>c</sup>  |
| 7 July                     | 50.9+5.8 <sup>a</sup> | 58.5+5.2 <sup>b</sup>  | 41.1+5.5 <sup>e</sup> | 58.9+4.6 <sup>b</sup> | 67.9+5.1 <sup>d</sup>  | 52.6+4.8 <sup>a</sup> | 68.5+7.4 <sup>d</sup>  |
| 6 Aug                      | 61.5+4.3 <sup>a</sup> | 89.1+6.2 <sup>b</sup>  | 54.6+4.0 <sup>d</sup> | 79.7+4.5 <sup>b</sup> | 103.8+7.3 <sup>c</sup> | 67.2+6.5 <sup>a</sup> | 106.7+7.7 <sup>c</sup> |
| Betula nana Production     |                       |                        |                       |                       |                        |                       |                        |
| 5 June                     | 11.7+2.6 <sup>a</sup> | 20.9+5.9 <sup>b</sup>  | 9.3+2.0 <sup>a</sup>  | 11.7+3.0 <sup>a</sup> | 13.3+2.7 <sup>ac</sup> | 15.8+3.9 <sup>c</sup> | 23.9+5.5 <sup>b</sup>  |
| 7 July                     | 17.1+4.2 <sup>a</sup> | 20.7+4.4 <sup>ab</sup> | 11.8+3.6 <sup>c</sup> | 16.7+3.4 <sup>a</sup> | 26.0+4.2 <sup>b</sup>  | 17.4+4.6 <sup>a</sup> | 28.4+6.0 <sup>b</sup>  |
| 6 Aug                      | 23.3+4.2 <sup>a</sup> | 27.3+5.5 <sup>b</sup>  | 15.7+3.0 <sup>c</sup> | 27.6+4.9 <sup>b</sup> | 27.6+4.9 <sup>b</sup>  | 20.3+3.6 <sup>a</sup> | 28.7+6.4 <sup>b</sup>  |
| Empetrum nigrum Production |                       |                        |                       |                       |                        |                       |                        |
| 7 July                     | 2.8+0.5 <sup>a</sup>  | 3.2+0.8 <sup>ac</sup>  | 1.8+0.4 <sup>b</sup>  | 2.6+0.6 <sup>a</sup>  | 3.7+1.0 <sup>c</sup>   | 2.0+0.3 <sup>b</sup>  | 3.6+0.9 <sup>c</sup>   |
| 6 Aug                      | 5.0+1.3 <sup>a</sup>  | 5.7+1.1 <sup>b</sup>   | 2.9+0.7 <sup>c</sup>  | 5.8+1.2 <sup>b</sup>  | 9.9+1.9 <sup>d</sup>   | 5.8+1.6 <sup>b</sup>  | 9.7+2.1 <sup>d</sup>   |







Table 5. Continued.

| Date   | Control               | 100N                   | 100P                  | Treatment                 |                       |                       |
|--------|-----------------------|------------------------|-----------------------|---------------------------|-----------------------|-----------------------|
|        |                       |                        |                       | 100N/100P                 | 200N                  | 200P                  |
|        |                       |                        |                       | <u>Monocot Production</u> |                       |                       |
| 5 June | 5.0+1.2 <sup>a</sup>  | 5.0+0.5 <sup>a</sup>   | 4.6+0.7 <sup>a</sup>  | 5.5+1.3 <sup>a</sup>      | 5.7+1.4 <sup>a</sup>  | 3.5+0.7 <sup>b</sup>  |
| 7 July | 10.1+1.3 <sup>a</sup> | 8.8+1.5 <sup>b</sup>   | 7.4+1.6 <sup>c</sup>  | 11.8+2.2 <sup>a</sup>     | 11.1+2.1 <sup>a</sup> | 7.9+1.1 <sup>c</sup>  |
| 6 Aug  | 10.6+1.5 <sup>a</sup> | 21.4+8.3 <sup>bc</sup> | 10.7+2.0 <sup>a</sup> | 15.5+3.4 <sup>b</sup>     | 14.3+1.8 <sup>b</sup> | 8.8+1.2 <sup>d</sup>  |
|        |                       |                        |                       |                           |                       | 23.9+4.8 <sup>c</sup> |

Values with the same superscript are not significantly different from each other at P=0.05 (Duncan's Multiple Range Test).



harvest. Betula nana, the first species to leaf out, accounted for a major portion of this increase. At the second harvest, the relative margins of increase in total production widened to 15% and 30% relative to the control, and to 45% and 68% at the time of the final harvest.

Monocot production, primarily Carex bigelowii, shows no difference at the first sampling period. By the final harvest, however, the same relationship is shown as with total and Betula production. Response to fertilizer application is thus dependent on the phenological characteristics of individual species, as is obvious in the case of Empetrum, which did not begin growth until the second harvest.

Phosphorus applied alone decreased total production by 20% at the low application rate, and increased production slightly (4%) at the high rate, at both the second and third harvests. This effect is generally mirrored in species production, and is especially evident in Carex, which was slow in responding to nitrogen, but showed a decrease under phosphorus application at the first harvest.

The low rate of nitrogen and phosphorus, applied in combination, increased total production by 15% and 30% at the second and third harvests, while the high rate resulted in increases of 35% and 75%. These values are significantly different from the control (Table 5), but not from nitrogen treatments.

The early response of Betula, Empetrum, and Carex to



combined application of nitrogen and phosphorus was variable. The high rate brought about an early stimulation of growth in all species, but this was not maintained at later sampling periods.

It appears from these results that in the dwarf shrub-heath community, total primary production is more strongly limited by the supply of available soil nitrogen than by phosphorus. The response to nitrogen and phosphorus fertilizer application relative to nitrogen alone at the first two harvests suggests a possible interaction between nitrogen and phosphorus metabolism and soil nutrition.

#### Physiological Response

Analyses of current Betula nana leaf material (Table 6) demonstrate that the observed increases in production are a direct consequence of the improved nutritional status of the soil. Under a low rate of nitrogen application, Betula shows a 20% increase in nitrate content, and a 180% increase at the high rate, at the second harvest. Nitrogen and phosphorus application results in increases of 90% at the low rate, and 60% at the high level of application. Although high resistance to water uptake as a result of low soil temperature was shown earlier, these results indicate that this resistance barrier does not prevent the uptake of nutrients if they are made available to the plant. Protein analyses from this sampling period show that incorporation of available nitrogen into organic compounds increases



Table 6. Results of chemical analyses of Betula nana current leaves;  
dwarf shrub-heath community near Tuktoyaktuk, N.W.T.

| Date     | Control | Treatment                          |      |           |           |
|----------|---------|------------------------------------|------|-----------|-----------|
|          |         | 100N                               | 100P | 100N/100P | 200N/200P |
|          |         | <u>Total protein- % dry weight</u> |      |           |           |
| 7 July   | 13.2    | 13.9                               | 12.9 | 15.4      | 18.5      |
|          |         |                                    |      | 12.8      | 16.6      |
| 5 August | 12.3    | 15.1                               | 12.7 | 14.7      | 16.3      |
|          |         |                                    |      | 11.7      | 16.4      |
|          |         | <u>Nitrate- % dry weight</u>       |      |           |           |
| 7 July   | 0.18    | 0.22                               | 0.15 | 0.32      | 0.44      |
|          |         |                                    |      | 0.14      | 0.28      |
| 5 August | 0.17    | 0.22                               | 0.21 | 0.45      | 0.44      |
|          |         |                                    |      | 0.20      | 0.41      |
|          |         | <u>Total fiber- % dry weight</u>   |      |           |           |
| 7 July   | 20.7    | 21.8                               | 20.9 | 21.2      | 20.2      |
|          |         |                                    |      | 18.4      | 20.9      |
| 5 August | 19.7    | 25.5                               | 21.8 | 23.5      | 22.1      |
|          |         |                                    |      | 21.7      | 19.5      |
|          |         | <u>Relative total flavonoids</u>   |      |           |           |
| 7 July   | 1.00    | 0.78                               | 0.85 | 0.64      | 0.56      |
|          |         |                                    |      | 0.87      | 0.47      |





Table 6. Continued.

| Date     | Control | 100N | 100P | Treatment                      |      |      |      |
|----------|---------|------|------|--------------------------------|------|------|------|
|          |         |      |      | 100N/100P                      | 200N | 200P |      |
|          |         |      |      | Total phosphorus- % dry weight |      |      |      |
| 7 July   | 0.20    | 0.21 | 0.27 | 0.27                           | 0.13 | 0.38 | 0.30 |
| 5 August | 0.27    | 0.29 | 0.61 | 0.49                           | 0.28 | 0.85 | 0.66 |



as well.

Soil temperature preceding this sampling period averaged approximately  $5^{\circ}\text{C}$  at -5 cm, and  $3^{\circ}\text{C}$  at -10 cm (Fig. 2). Dadykin (1958) has reported strong inhibition of both uptake and incorporation of nitrogen in wheat grown at  $3^{\circ}\text{C}$ , but it appears that inhibition of either uptake or incorporation is of less importance with these native plants under field conditions. Direct inhibition of metabolism by temperature is not the major limiting factor in these native plants.

This is further supported by the flavonoid content of Betula nana under fertilizer application. A high flavonoid content, manifested in a high anthocyanin content resulting in a reddening of petioles, leaf veins, and leaf margins, has been used as a visible indication of nitrogen deficiency in crop plants in temperate regions (American Society of Agronomy, 1941), and was observed in the field in several control species. Total relative flavonoid content, including anthocyanins, flavones, and flavonols, shows a decrease under all treatments relative to the control (Table 6), but more markedly so in the case of nitrogen and nitrogen and phosphorus application, flavonoid content decreasing proportional to the rate of application. It thus appears that, relative to norms established for temperate plants, tundra ecosystems may exist under a partial state of nitrogen deficiency, at least in part responsible for the low levels of primary production.



Uptake of phosphorus does not appear to be strongly limited under field conditions, as total phosphorus content of Betula leaves increases under all phosphorus applications, contrary to the results obtained by Shtrausberg (1958) with agronomic species. This confirms the results of Korovin et al. (1963) in which they reported a large increase in total phosphorus content of phosphorus fertilized plants grown at low temperatures. Although total phosphorus content increased, plant production remained about the same, while protein content decreased. Although phosphorus can be taken up, it appears not to be incorporated into organic compounds at low temperature (Korovin et al., 1963; Kursanov and Kulaeva, 1957).

Increased incorporation into phosphate esters (ATP, glucose-6-P) would bring about an increase in cyclic phosphorylation and increased production, which did not occur. Increased incorporation into nucleoproteins would result in increased protein transcription and thus protein content, which also was not observed in phosphorus treated plants.

The process of phosphorus incorporation may be somewhat limited by the supply of available nitrogen. A low rate of application of nitrogen and phosphorus in combination showed a slight increase in protein content relative to the low rate of nitrogen application. However, at a high rate of nitrogen and phosphorus application, this was not





observed. Thus the limitation of phosphorus incorporation by available nitrogen level, while perhaps to some degree limiting to growth and production, is not a major limiting mechanism in this community.

It appears that low temperature acts directly on the plant to inhibit incorporation of phosphorus into organic compounds, particularly nucleoproteins, while the uptake of phosphorus is relatively unaffected. This confirms, to some extent, the findings of Soviet workers (Zhurbitsky and Shtrausberg, 1958; Korovin et al., 1963). However, contrary to the earlier studies, a large application of phosphorus as a fertilizer, even in combination with nitrogen, does not increase production, indicating that the barrier to incorporation is an extremely strong one, or that phosphorus is not quantitatively limiting in this soil.

#### Nutrient-Temperature Interactions

Results of hydroponic culture experiments with Lupinus demonstrate the interaction between temperature and nitrogen nutrition, and may help to explain the limitations to production which exist in the field. From the results for root and shoot elongation (Figs. 5, 6 ), it can be seen that growth is strongly related to both temperature and nutrition level. At relatively high temperatures ( $15^{\circ}\text{C}$ ), there is a direct relationship shown with nitrate nitrogen level such as was observed in the field (Fig. 5a). At  $5^{\circ}\text{C}$ , however,

Figure 5a. Lupinus arcticus shoot growth at 15<sup>o</sup>C and varying nitrogen levels.

Figure 5b. Lupinus arcticus shoot growth at 5<sup>o</sup>C and varying nitrogen levels.



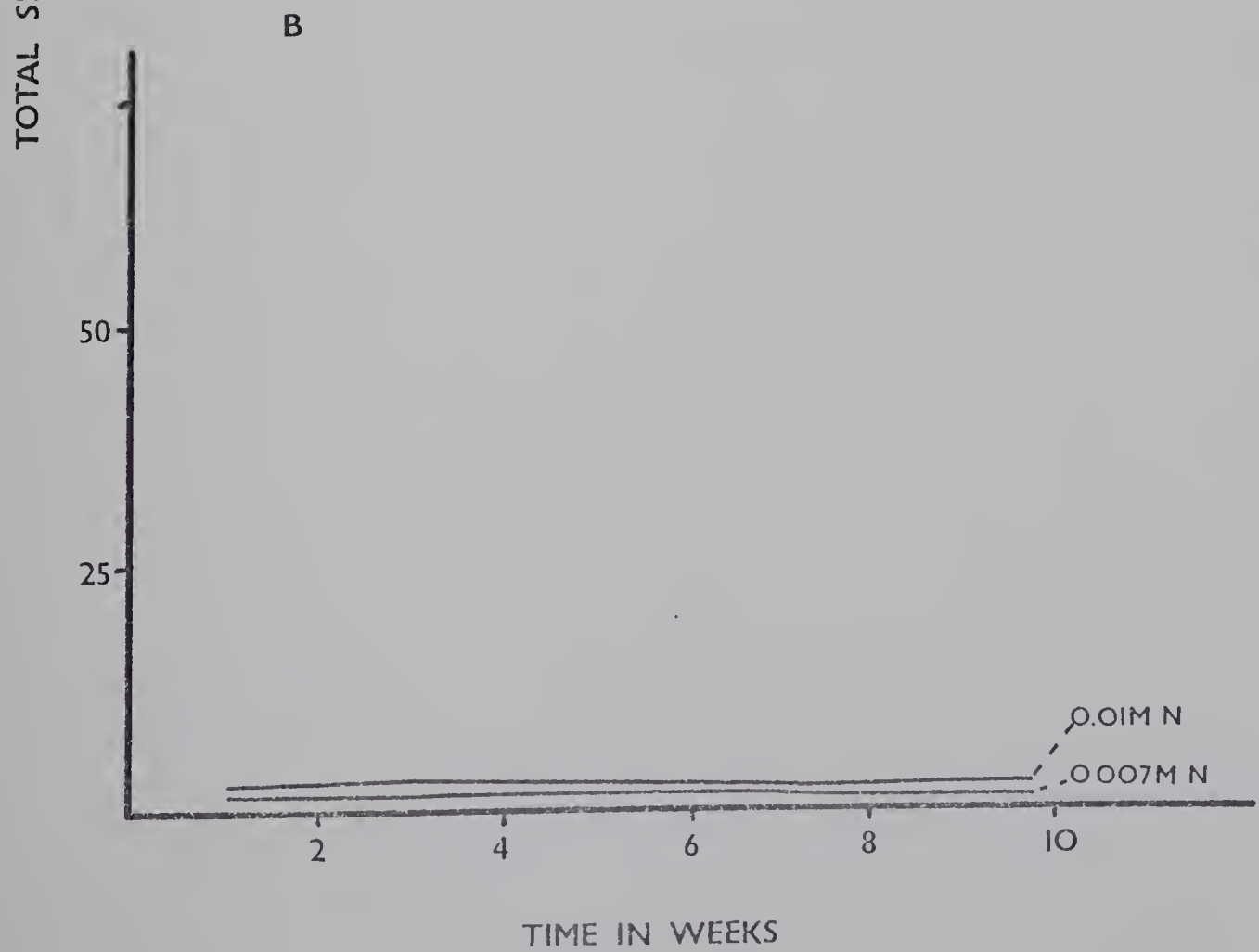
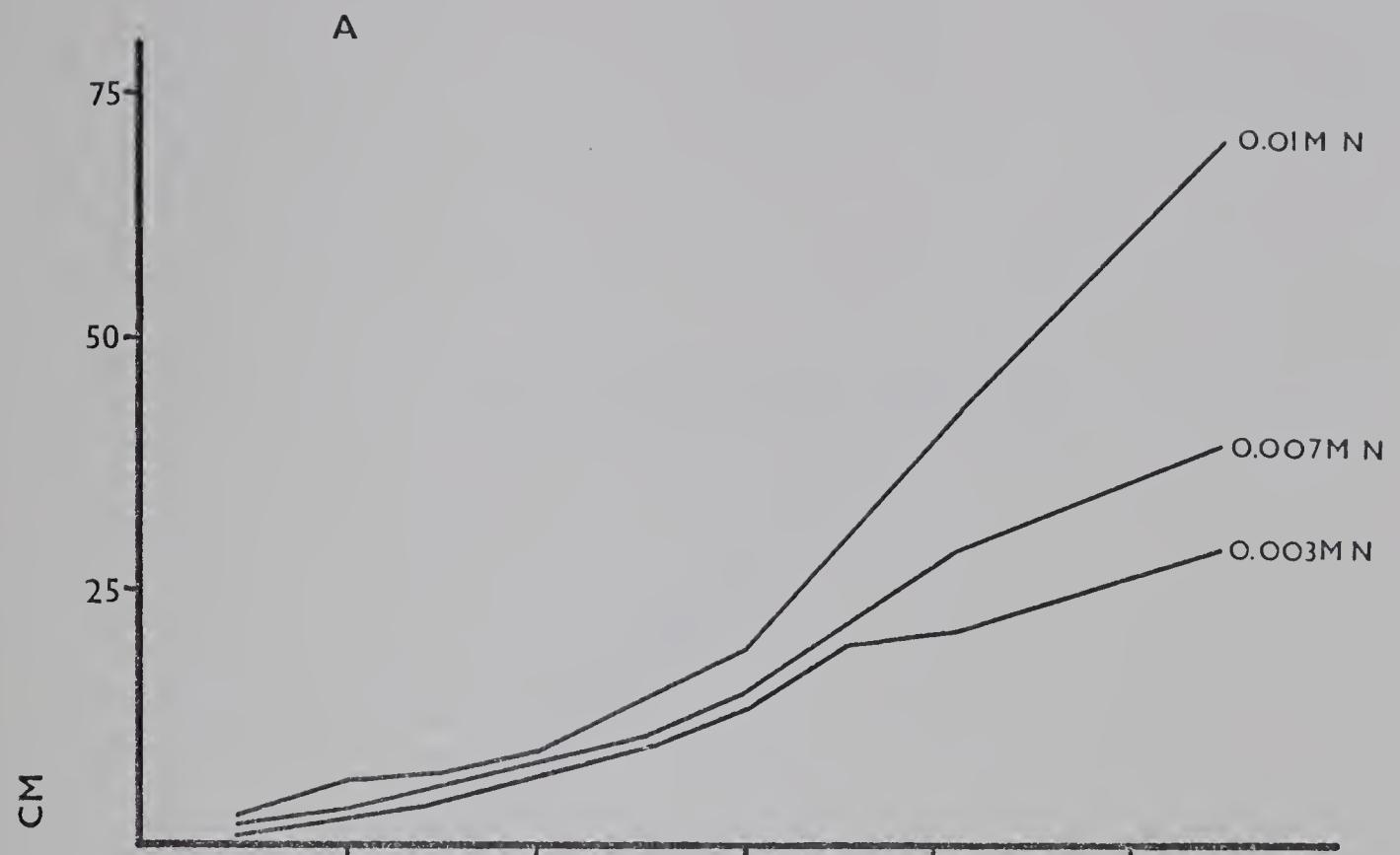
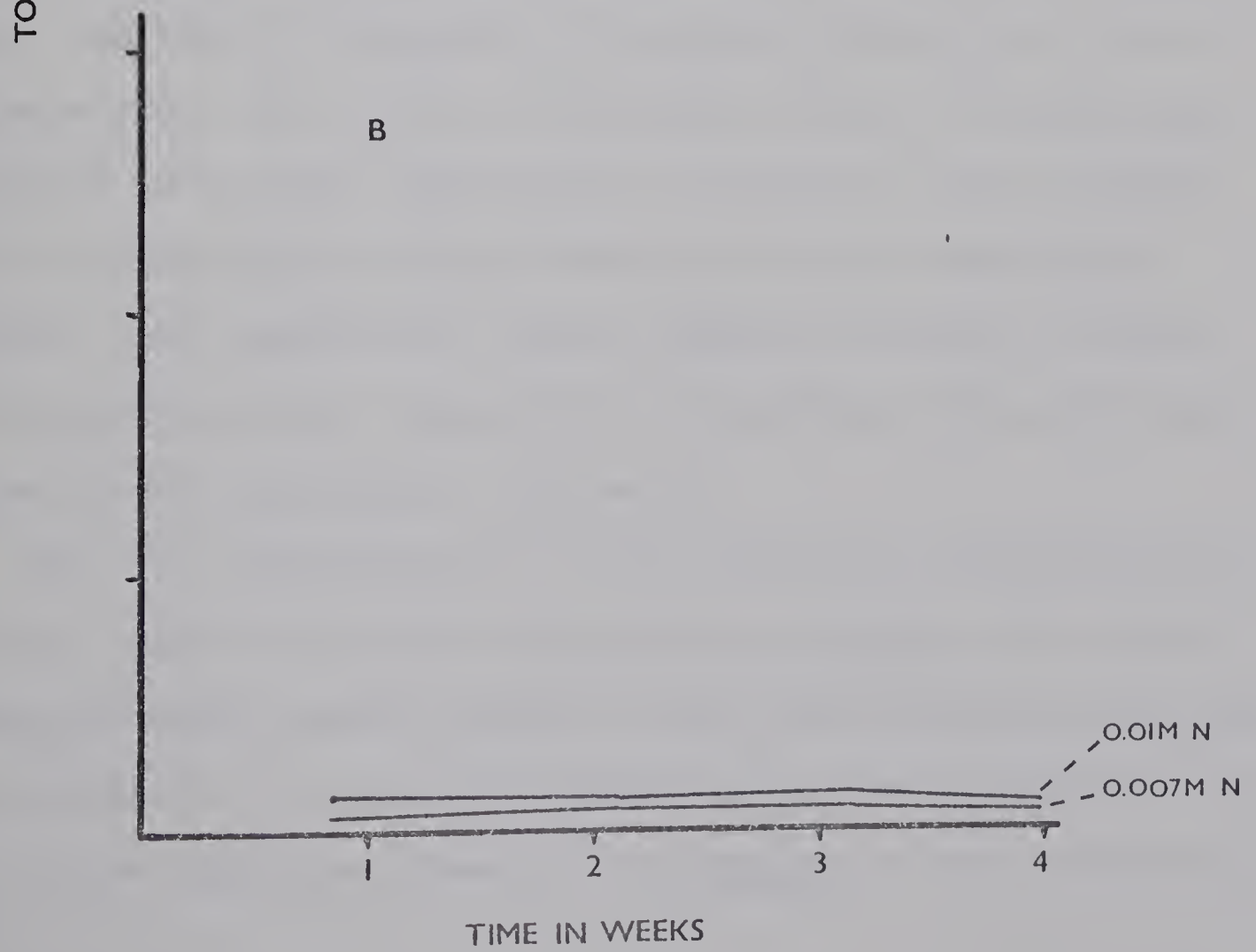
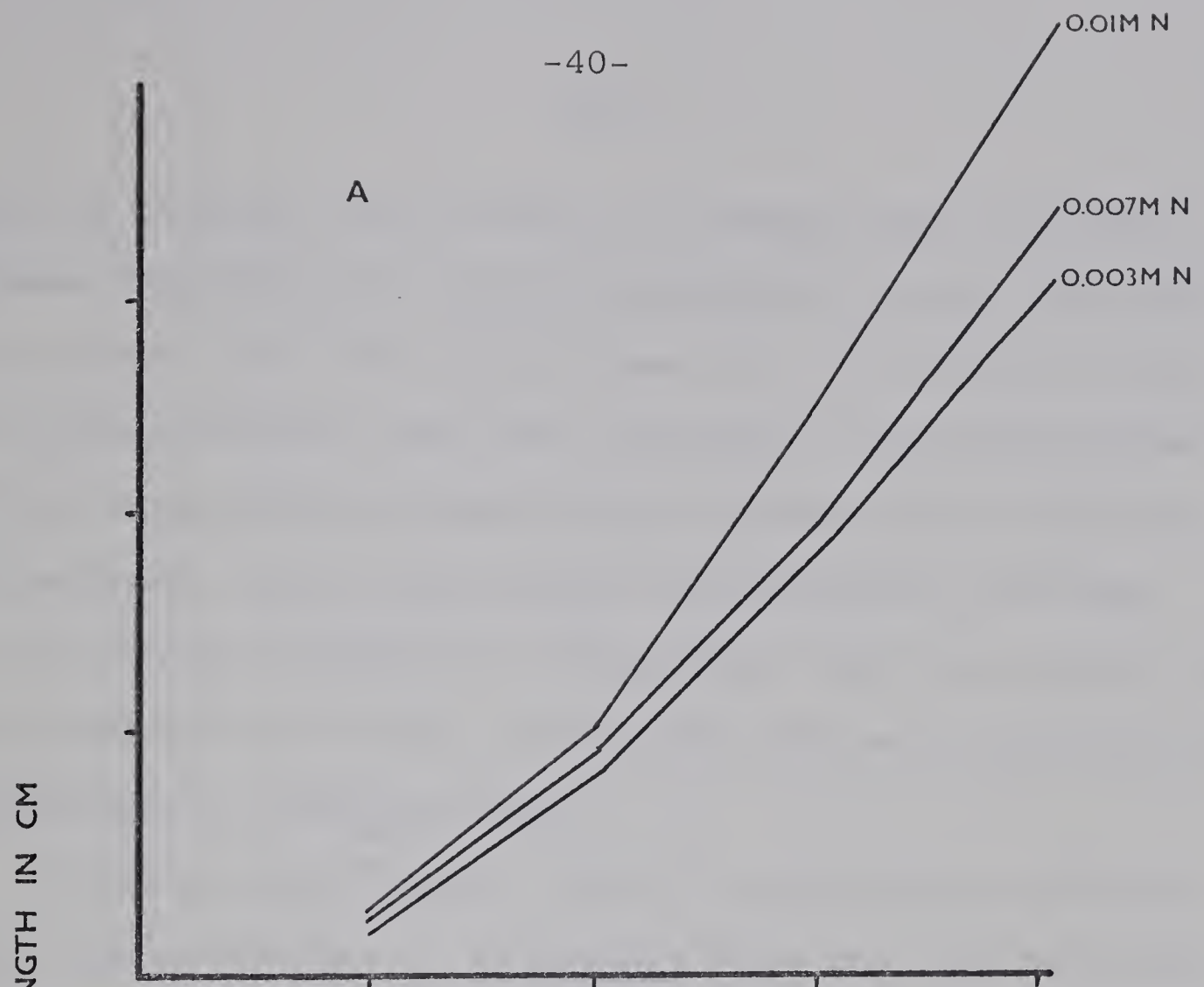


Figure 6a. Lupinus arcticus root growth at 15<sup>o</sup> C and  
varying nitrogen levels.

Figure 6b. Lupinus arcticus root growth at 5<sup>o</sup> C and  
varying nitrogen levels.





there is no such relationship, as growth does not differ between the 0.01 and 0.007 M nutritional levels. The fact that plants under the 0.003 M level at 5°C failed to grow at all may indicate that the limitation to growth imposed at low temperature by low nitrogen levels exists only as a threshold value, above which physiological processes are so strongly limited by temperature that these become the rate determining factors, and growth proceeds relatively independently of nitrogen level.

Fresh and dry weights (Table 7) and relative chlorophyll content (Table 8) in Lupinus show the same relationship with temperature and nutrition level as does growth. The variation in chlorophyll content at 15°C demonstrates a direct limitation by nutrition level on chlorophyll production, and thus a limitation on primary production. At low temperatures, the effect of nutrition level on primary metabolism is of less importance, as there is little difference in chlorophyll content between the two nutritional levels. Low temperature itself appears to exert an important and overriding limitation on production through inhibition of net chlorophyll synthesis.

The low temperatures in this laboratory experiment appear to inhibit nitrogen metabolism in Lupinus, but the response of other plant species in the field demonstrates that the limitation of nitrogen metabolism by low temperature is not of the magnitude observed for Lupinus in the laboratory.



Table 7. Fresh and dry weight production (g) over 10 weeks of Lupinus arcticus in relation to temperature and nitrogen nutrition (mean  $\pm$  standard error).

| Temp              | NO <sub>3</sub> | Shoot fresh      | Shoot dry       | Root fresh       | Root dry        |
|-------------------|-----------------|------------------|-----------------|------------------|-----------------|
| 15 <sup>o</sup> C | 0.01M           | 12.23 $\pm$ 4.31 | 4.50 $\pm$ 1.53 | 27.38 $\pm$ 4.40 | 4.50 $\pm$ 0.98 |
| "                 | 0.007M          | 4.66 $\pm$ 1.35  | 1.12 $\pm$ 0.46 | 14.97 $\pm$ 3.62 | 1.26 $\pm$ 0.27 |
| "                 | 0.003M          | 3.88 $\pm$ 0.85  | 0.56 $\pm$ 0.39 | 11.32 $\pm$ 1.71 | 1.46 $\pm$ 0.68 |
| 5 <sup>o</sup> C  | 0.01M           | 0.20 $\pm$ 0.11  | 0.06 $\pm$ 0.01 | 0.33 $\pm$ 0.26  | 0.06 $\pm$ 0.02 |
| "                 | 0.007M          | 0.13 $\pm$ 0.03  | 0.06 $\pm$ 0.01 | 0.43 $\pm$ 0.17  | 0.06 $\pm$ 0.01 |

Table 8. Absorbance of chlorophyll extracts of equivalent weight samples of Lupinus arcticus leaf tissue in relation to temperature and nitrogen nutrition (values are absorbance at designated wavelength)

| Temp              | NO <sub>3</sub> | A <sub>445</sub> | A <sub>665</sub> | <u>Sum</u> | A <sub>470</sub> | A <sub>615</sub> | <u>Sum</u> | Total |
|-------------------|-----------------|------------------|------------------|------------|------------------|------------------|------------|-------|
| 15 <sup>o</sup> C | 0.01M           | .076             | .046             | .122       | .056             | .018             | .074       | .196  |
| "                 | 0.007M          | .066             | .042             | .108       | .047             | .013             | .060       | .168  |
| "                 | 0.003M          | .055             | .032             | .087       | .036             | .009             | .045       | .132  |
| 5 <sup>o</sup> C  | 0.01M           | .033             | .017             | .050       | .022             | .005             | .027       | .077  |
| "                 | 0.007M          | .033             | .016             | .049       | .040             | .005             | .045       | .094  |





Flavonoid content, previously mentioned as an empirical indicator of nitrogen deficiency, yields useful information regarding the physiological status of the plant with respect to nitrogen metabolism. The flavonoid synthetic pathway is directly linked to nitrogen metabolism during the formation of the 15 carbon skeleton common to all flavonoid compounds. The A ring of this skeleton is formed from the head to tail condensation of two malonyl and one acetyl co-A molecules, which is then joined to an aromatic B ring and central 3 carbon unit. This B ring can be derived in a number of ways, commonly from the direct hydroxylation of phenylalanine (Harborne, 1967) or tyrosine (Hewitt et al., 1968).

Dadykin (1958) reported a quantitative equilibrium in amino acid content of plants, based on the energy of formation; the neutral aliphatic acids are easily synthesized, and thus present in largest quantity, followed by the aliphatic acidic and basic amino acids. The aromatic amino acids, including phenylalanine and tyrosine, are more complex and require a higher energy input, and are thus present in lower quantities.

Absorbance of flavonoid extracts of equivalent samples, a measure of relative flavonoid content, is presented in Table 9. It can be seen that at high temperature, UV absorbance by flavonoid compounds is relatively low for all treatments, indicating a low flavonoid content.



Table 9. Absorbance of flavonoid extracts of equivalent weight samples of Lupinus arcticus leaf tissue in relation to temperature and nitrogen nutrition.

| Temp | NO <sub>3</sub> | A <sub>262 nm</sub> | A <sub>337 nm</sub> | Total |
|------|-----------------|---------------------|---------------------|-------|
| 15°C | 0.01 M          | 0.292               | 0.143               | 0.435 |
| "    | 0.007 M         | 0.242               | 0.109               | 0.353 |
| "    | 0.003 M         | 0.243               | 0.091               | 0.334 |
| 5°C  | 0.01 M          | 0.317               | 1.100               | 1.147 |
| "    | 0.007 M         | 0.420               | 1.105               | 1.525 |

Between 0.007 and 0.003 M nitrogen, there is little difference, while at 0.01 M, there is a slight increase.

Under conditions of high nitrogen nutrition, nitrate is taken up by the roots and transported directly to the leaves, which then synthesize the majority of amino acids required by the plant (Pate, 1968). Under such conditions, the typical photosynthetic amino acids, including glycine and serine, are produced at a rate directly proportional to the photosynthetic capacity of the plant, and relatively independent of nitrogen level. The rate of protein synthesis is thus not dependent on the rate of production of these quantitatively major constituents of protein, but on the rate of production of more complex amino acids.

Under conditions of low nitrogen nutrition, nitrate is not generally transported directly to the leaves; the root serves as the site of reduction of inorganic nitrogen and



production of many amino acids, using sucrose supplied by the leaf as the source of carbon. The amino and amido groups produced in the root, primarily as glutamine, then serve as the principle source of reduced organic nitrogen for production of additional amino acids in the photosynthesizing leaf (Pate and Grieg, 1964; Pate, 1968).

At 0.01 M nitrogen, flavonoids show an increase relative to both 0.007 and 0.003 M. Chlorophyll content is high (Table 8); the supply of nitrate to the leaf thus appears in excess of the capacity of the plant to produce photosynthetic amino acids. The excess nitrate is incorporated into complex amino acids at a level above that required for utilization in protein synthesis. The excess amino acids then become available for increased flavonoid synthesis, with the flavonoid compounds functioning as a sink for excess carbohydrate, as hypothesized by Billings and Mooney (1968).

Relative total flavonoid content of both treatments at 5°C is 3 to 4 times that at 15°C, and shows no relationship with nutrition level. The high flavonoid content is evidence for production of aromatic amino acids at low temperature, contrary to the results of Dadykin (1958) with crop species.

The direct decrease in chlorophyll content at low temperature is, at least in part, responsible for the increase in flavonoid content. This results in a low rate of forma-





tion of photosynthetic amino acids, which become quantitatively limiting to protein synthesis. The excess nitrogen is again diverted into more complex amino acids, and becomes available to the flavonoid synthetic pathway, functioning as a carbohydrate sink. Production at low temperature ( $5^{\circ}\text{C}$ ) is thus relatively independent of nitrogen concentration in the substrate with Lupinus.

A comparison with results obtained with Betula nana in the field demonstrates that the limitation of nitrogen metabolism by low temperature is not significant. Addition of inorganic nitrogen fertilizer brought about a reduction in flavonoid content, as well as an increase in production. This shows that the direct limitation of chlorophyll synthesis by nitrogen level, which was demonstrated in the laboratory, is an important limiting mechanism in the field. As available nitrogen increased, so did chlorophyll content, resulting in increased capacity for production of photosynthetic amino acids. The pool of excess aromatic amino acids resulting in a high flavonoid content at low nutrition levels, could thus be utilized in protein synthesis, resulting in both increased protein content and decreased flavonoid content observed under nitrogen application.

The increase in both production and protein content, and marked decrease in flavonoid content, shown by Betula nana in the field, and the lack of such response by Lupinus arcticus at low temperature in the laboratory, demonstrate





that at air and soil temperatures encountered in the field, the physiological limitation of nitrogen incorporation by low temperature is not a major limiting mechanism for many native species. Increased nitrate content of Betula under mineral fertilization demonstrates that uptake is not strongly limited by temperature either.

#### Wet Sedge Meadow Community

##### Soil Nutrient Status

Results of soil nutrient analyses are presented in Table 10. Available nitrogen was not determined in this community, due to the high organic content of the soil. Available soil phosphorus is somewhat less in the control plots in this community relative to the dwarf shrub-heath. Phosphorus enters a system primarily through chemical weathering of soil minerals. Peat extends below the maximum depth of the active layer in this community, and thus mineral soil is never exposed to weathering conditions. This probably accounts for the low soil values, and we might expect the quantity of phosphorus to be more strongly limiting to growth here than in the dwarf shrub-heath community.

Phosphorus availability has been shown to vary in organic soils in relation to soil water saturation (Saebø, 1968, 1970). Increasing soil wetness results in dilution of the soil solution and consequent decrease in phosphorus availability (Overstreet and Dean, 1951; Lagerwerff, 1958),



Table 10. Results of chemical analyses of organic soil from the wet sedge meadow community near Tuktoyaktuk, N.W.T.

| Date                       | Depth (cm) | Control | Treatment |       |           | 200N  | 200P  | 200N/200P |
|----------------------------|------------|---------|-----------|-------|-----------|-------|-------|-----------|
|                            |            |         | 100N      | 100P  | 100N/100P |       |       |           |
| Total nitrogen (%)         |            |         |           |       |           |       |       |           |
| 16 July                    | 0-10       | 2.36    | 2.44      | 2.58  | 2.31      | 2.54  | 2.07  | 2.31      |
|                            | 10-20      | 2.66    | 1.99      | 2.53  | 2.31      | 2.49  | 2.39  | 2.25      |
| 7 August                   | 0-10       | 2.40    | 2.23      | 2.43  | 2.27      | 2.40  | 2.37  | 2.48      |
|                            | 10-20      | 2.48    | 2.16      | 2.43  | 2.41      | 2.62  | 2.50  | 2.68      |
| Available phosphorus (ppm) |            |         |           |       |           |       |       |           |
| 16 July                    | 0-10       | 6.0     | 8.0       | 16.0  | 42.5      | 9.5   | 63.0  | 81.0      |
|                            | 10-20      | 3.0     | 3.0       | 2.0   | 4.0       | 4.5   | 5.0   | 20.0      |
| 7 August                   | 0-10       | 4.0     | 7.0       | 15.0  | 21.5      | 6.5   | 34.5  | 55.0      |
|                            | 10-20      | 3.0     | 2.0       | 3.0   | 2.5       | 2.0   | 4.0   | 8.0       |
| Available calcium (ppm)    |            |         |           |       |           |       |       |           |
| 16 July                    | 0-10       | 625.0   | 590.0     | 810.0 | 585.0     | 625.0 | 717.0 | 690.0     |
|                            | 10-20      | 970.0   | 655.0     | 810.0 | 842.0     | 495.0 | 850.0 | 810.0     |
| 7 August                   | 0-10       | 650.0   | 685.0     | 715.0 | 700.0     | 620.0 | 637.0 | 775.0     |
|                            | 10-20      | 775.0   | 785.0     | 685.0 | 905.0     | 932.0 | 667.0 | 1025.0    |



Table 10. Continued.

| Date      | Depth (cm) | Control | Treatment |      |           |      |      |           |
|-----------|------------|---------|-----------|------|-----------|------|------|-----------|
|           |            |         | 100N      | 100P | 100N/100P | 200N | 200P | 200N/200P |
| <u>PH</u> |            |         |           |      |           |      |      |           |
| 16 July   | 0-10       | 5.2     | 5.6       | 5.1  | 5.3       | 5.7  | 5.0  | 5.2       |
|           | 10-20      | 5.3     | 5.2       | 5.4  | 5.3       | 5.6  | 5.3  | 5.3       |
| 7 August  | 0-10       | 5.0     | 5.8       | 5.1  | 5.4       | 6.1  | 5.3  | 4.8       |
|           | 10-20      | 5.1     | 4.9       | 5.4  | 5.1       | 5.5  | 5.3  | 5.1       |



which may also be a factor in this soil.

Soil pH is slightly higher in this Carex peat than in the Gleysol. This may reflect the level of microbial activity, since carbohydrate decomposing bacteria tend to lower the pH (Alexander, 1961). Thus the unexpectedly higher pH in this soil may indicate a lower level of microbial activity.

Values for available calcium are extremely high; it is unlikely that this element is limiting to production.

#### Community Production

The application of nitrogen, both at low and high rates, singly and in combination with phosphorus, resulted in large increases in production at the first harvest, becoming even larger at later sampling periods, which differ significantly from the control at  $P=0.05$  (Table 11). The results of nitrogen application relative to nitrogen and phosphorus do not differ significantly until the third harvest, at which time nitrogen and phosphorus application can be seen to bring about a significantly larger increase in production than nitrogen applied alone ( $P=0.05$ ).

From this we can infer that available nitrogen supply in this soil is extremely limited. Additionally, there does not appear to be the direct relationship between nitrogen and calcium availability which Gore (1963) implied in the interpretation of results of mineral fertilization experiments in bog communities.





Table 11. Total above ground dry weight production (g/m<sup>2</sup>) in  
a wet sedge meadow community near Tuktoyaktuk, N.W.T.

| Date     | Control               | 100N                    | Treatment             |                        |                        |                                              |
|----------|-----------------------|-------------------------|-----------------------|------------------------|------------------------|----------------------------------------------|
|          |                       |                         | 100P                  | 100N/100P              | 200N                   | 200P 200N/200P                               |
| 25 June  | 51.3+2.7 <sup>a</sup> | 76.7+7.6 <sup>b</sup>   | 44.6+5.7 <sup>c</sup> | 71.3+5.9 <sup>b</sup>  | 55.3+10.0 <sup>a</sup> | 57.6+3.1 <sup>ad</sup> 63.0+2.6 <sup>d</sup> |
| 16 July  | 60.7+2.8 <sup>a</sup> | 115.2+6.1 <sup>b</sup>  | 60.9+4.8 <sup>a</sup> | 119.3+8.4 <sup>b</sup> | 91.0+6.9 <sup>c</sup>  | 61.2+1.6 <sup>a</sup> 78.8+11.1 <sup>d</sup> |
| 7 August | 72.5+6.9 <sup>a</sup> | 139.0+13.3 <sup>b</sup> | 59.9+8.2 <sup>c</sup> | 181.5+6.7 <sup>d</sup> | 118.0+2.9 <sup>e</sup> | 54.1+5.5 <sup>c</sup> 138.6+9.9 <sup>b</sup> |

Values with the same superscript are not significantly different from each other at P=0.05 (Duncan's Multiple Range Test).



Saebø (1968) stated that phosphorus may be the most severely limiting element in bog communities. In mineral fertilization experiments in bog communities Gore (1961a) and Tamm (1954) have demonstrated increases in Eriophorum vaginatum production with phosphorus addition.

Phosphorus addition, however, failed to bring about any increase in production, and in fact caused a decrease (Table 11). Thus phosphorus does not appear to be quantitatively limiting to production in this community.

Nitrogen and phosphorus fertilization did not result in a relative increase over nitrogen at the first two harvests. However, the significant increase at the third harvest indicates that phosphorus utilization in this community may be strongly tied to the availability of nitrogen.

#### Physiological Response

Plant nitrate content increased greatly in plants receiving nitrogen as fertilizer (Table 12). The rapid uptake of nitrogen resulting in large nitrate differences at the first harvest occurs despite the high resistance to water uptake noted earlier. Inhibition of nutrient uptake by low soil temperatures of approximately 6°C (Fig. 7) does not appear to be a major limiting mechanism in this community.

Total protein content shows a 100% increase in nitrogen treated vs. control plots, which is maintained throughout the growing season. This indicates that nitrogen metabolism



Table 12. Results of chemical analyses on total production material from wet sedge meadow community near Tuktoyaktuk, N.W.T.

| Date                              | Control | 100N | Treatment |           |      | 200N | 200P | 200N/200P |
|-----------------------------------|---------|------|-----------|-----------|------|------|------|-----------|
|                                   |         |      | 100P      | 100N/100P | 200N |      |      |           |
| <u>Total protein-% dry weight</u> |         |      |           |           |      |      |      |           |
| 25 June                           | 10.0    | 20.1 | 13.3      | 22.4      | 26.2 | 8.1  |      | 21.8      |
| 16 July                           | 10.3    | 15.6 | 11.5      | 18.4      | 21.6 | 11.9 |      | 19.6      |
| 7 August                          | 8.0     | 14.3 | 9.8       | 16.2      | 20.9 | 9.5  |      | 19.1      |
| <u>Nitrate- % dry weight</u>      |         |      |           |           |      |      |      |           |
| 25 June                           | 0.15    | 0.92 | 0.12      | 0.96      | 5.23 | 0.06 |      | 0.48      |
| 16 July                           | 0.29    | 0.30 | 0.34      | 0.34      | 1.23 | 0.20 |      | 0.34      |
| 7 August                          | 0.30    | 0.42 | 0.27      | 0.40      | --   | 0.27 |      | 0.42      |
| <u>Total fiber- % dry weight</u>  |         |      |           |           |      |      |      |           |
| 16 July                           | 28.7    | 18.9 | 29.6      | 24.4      | 16.9 | 30.6 |      | 17.6      |
| 7 August                          | 30.7    | 28.0 | 29.4      | 26.3      | 22.3 | 31.6 |      | 26.8      |

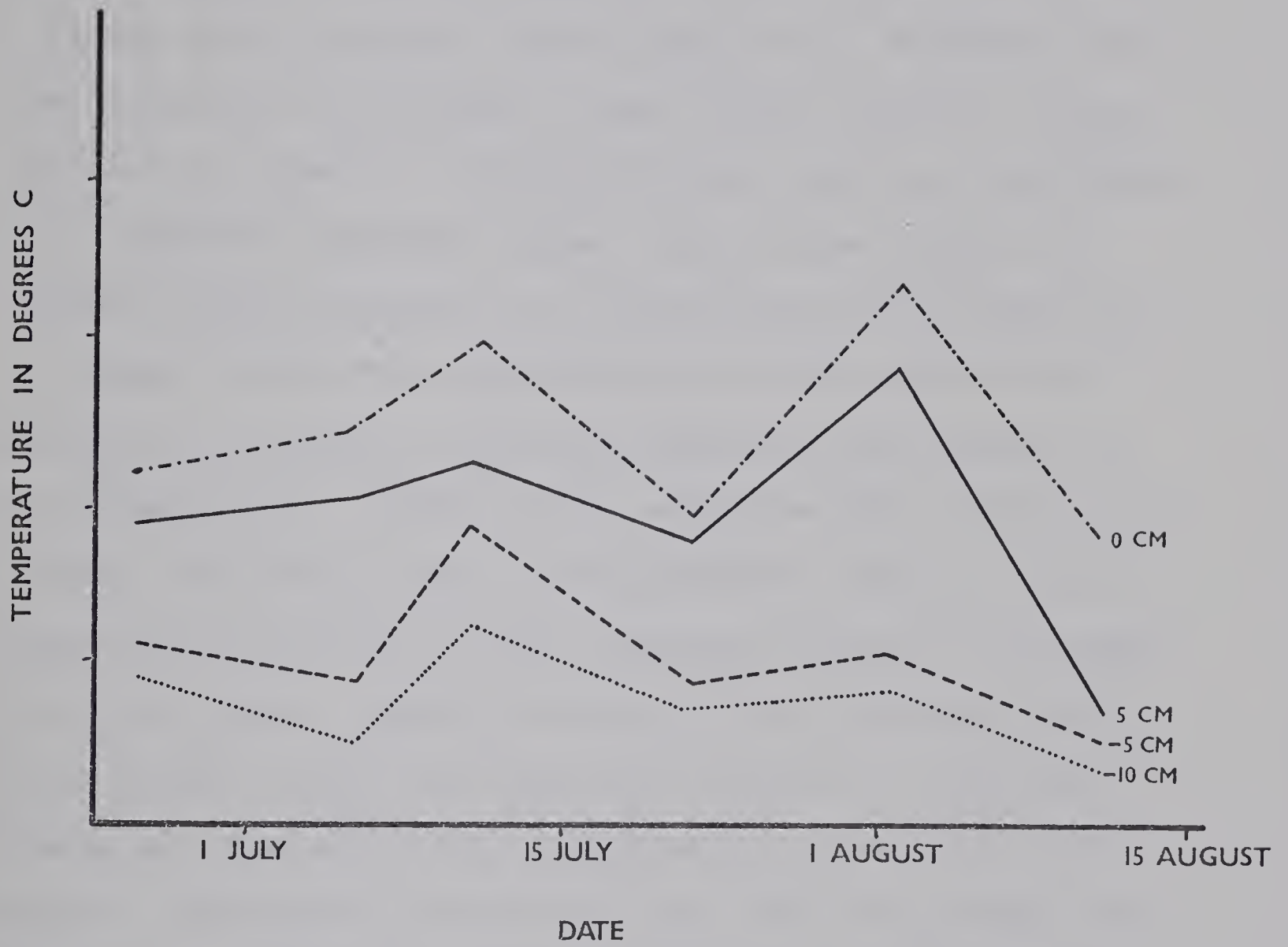


Table 12. Continued.

| Date                                  | Control | 100N | Treatment |           |      |      |           |
|---------------------------------------|---------|------|-----------|-----------|------|------|-----------|
|                                       |         |      | 100P      | 100N/100P | 200N | 200P | 200N/200P |
| <u>Total phosphorus- % dry weight</u> |         |      |           |           |      |      |           |
| 25 June                               | 0.13    | 0.18 | 0.89      | 0.53      | 0.26 | 0.78 | 0.80      |
| 16 July                               | 0.12    | 0.14 | 0.89      | 0.46      | 0.20 | 1.20 | 0.72      |
| 7 August                              | 0.09    | 0.34 | 0.32      | 0.37      | 0.31 | 0.76 | 0.94      |
| <u>Total potassium- % dry weight</u>  |         |      |           |           |      |      |           |
| 25 June                               | 0.50    | 0.69 | 1.12      | 0.84      | 0.77 | 1.00 | 1.56      |
| 16 July                               | 1.07    | 1.17 | 1.29      | 1.17      | 1.08 | 1.62 | 1.34      |
| 7 August                              | 0.96    | 0.87 | 0.83      | 0.66      | --   | 1.18 | 1.16      |
| <u>Total calcium- % dry weight</u>    |         |      |           |           |      |      |           |
| 25 June                               | 0.23    | 0.21 | 0.29      | 0.24      | 0.27 | 1.50 | 0.37      |
| 16 July                               | 0.23    | 0.17 | 0.19      | 0.30      | 0.23 | 0.41 | 0.31      |
| 7 August                              | 0.24    | 0.26 | 0.37      | 0.49      | --   | 0.37 | 0.51      |

Figure 7. Seasonal variation in air and soil temperature profiles in a wet sedge meadow community near Tuktoyaktuk, N.W.T.







is not inhibited by low soil temperatures, confirming results from the dwarf shrub-heath community.

As is the case in the drier heath-shrub community, the low supply of available soil nitrogen appears to be a factor which strongly limits production. Evidence from the literature is variable. Gore (1961b) reports a small increase in growth in fertilized plots which he attributes to an improved nitrogen regime, while Saebø (1970) obtained variable results in an ombrotrophic bog community.

Other authors have speculated as to the major role played by nitrogen in limiting growth and development in bog communities. Firbas (1931) suggested that certain xeromorphic characters common to bog species, such as thickened cuticles and cell walls, might be related to nitrogen nutrition level. Under conditions of low nitrogen nutrition, Miller (1963) has shown that products of photosynthesis are channeled into the formation of cell wall products. He further hypothesized that the low nitrogen regime of organic soils is reinforced by low soil temperatures, impairing the ability of the plant to absorb and utilize nitrogen. Other evidence (Shtrausberg, 1958), as well as the results of the present study, have shown the latter to be a minor factor under field conditions.

Total fiber content of sedge meadow current growth decreases appreciably under nitrogen fertilization (Table 12), although there is no consistent pattern within the treat-



ments themselves. The high dry weight proportion of fiber suggests xeromorphy, as stated by Miller (1963) due to the low nitrogen status of the soil. This xeromorphy does not appear reinforced by low soil temperature, as shown by the decrease in fiber content under nitrogen addition, also observed by Müller-Stoll (1948) with Eriophorum vaginatum. The reversability of this xeromorphy also indicates that it is a phenotypic, rather than genetic, characteristic. Implications of this are discussed later.

Phosphorus uptake does not appear strongly limited by low soil temperature. Total phosphorus content of plants in plots fertilized with phosphorus or phosphorus and nitrogen shows a large increase at the first harvest relative to the control (Table 12). In plants receiving phosphorus only there is a peak in phosphorus content at the second harvest, and a decline thereafter. Apparently this is a result of senescence, with phosphorus being retranslocated to below ground storage organs, observed for other species in similar habitats (Saebø, 1970). While phosphorus content of control and phosphorus treated plants drops off by the third harvest, both nitrogen and nitrogen and phosphorus treatments fail to show such a decrease, and in fact continue to rise. It thus appears that senescence may be delayed by an improvement in nitrogen nutrition.

Korovin et al. (1963) and Zhurbitsky and Shtrausberg





(1954, 1958) have observed a major limitation to phosphorus incorporation by low soil temperature, which was noted earlier. Incorporation, particularly into nucleoproteins, is greatly reduced under low soil temperatures, in turn implying an important relationship with nitrogen metabolism, another major constituent of nucleoproteins.

While there is a large increase in total phosphorus in plants receiving phosphorus alone, there is no increase in either production or protein content. Phosphorus incorporation thus appears limited in this community by soil temperature and low available nitrogen levels.

Application of nitrogen and phosphorus in combination shows, for the first two harvests, substantially the same increase in production as with nitrogen alone. A low rate of nitrogen and phosphorus application results in increased protein content relative to nitrogen application, while phosphorus content of all plants receiving nitrogen shows an increase over the control at both levels throughout the growing season.

By the third harvest, nitrogen and phosphorus application does show a significantly larger production increase than nitrogen applied alone ( $P=0.05$ ). These results indicate an additional important effect of low soil nitrogen, in the limitation of phosphorus incorporation into functional organic compounds.

The fact that major differences between nitrogen and





nitrogen and phosphorus treatments only became evident by the third harvest suggests that the limitation of phosphorus availability by soil moisture levels may be an important factor in the wet sedge meadow community. Only as the soil dried somewhat late in the growing season did the concentration of available phosphorus rise sufficiently to show any effect on production

Low phosphorus content in the soil has been shown to affect nitrogen metabolism as well, for ammonium is bound to compounds not characteristic of normal plants (Kursanov and Kulaeva, 1957), and is thus unavailable for amino acid synthesis. Increase in protein content under a low rate of nitrogen and phosphorus fertilization relative to nitrogen alone indicates that this mechanism may limit production. Lack of the same relationship at high rates of fertilizer application shows this to be a minor factor.

These results demonstrate that the availability of soil nitrogen is a major factor in the limitation of production in this community. The plants appear able to absorb and utilize nitrogen under field conditions, but the supply of available nitrogen is limited by other environmental factors. Incorporation of nitrogen may be somewhat limited by the availability of phosphorus. This, however, is a minor factor.

The quantity of phosphorus in the soil does not appear to limit plant growth. There may be a direct limitation by



temperature of incorporation into organic compounds, as was suggested in the heath-shrub community.

The increase in production with nitrogen and phosphorus relative to nitrogen fertilizer application and the increase in protein content indicate that, in the wet sedge meadow, the major factor limiting phosphorus incorporation is the low supply of available nitrogen.



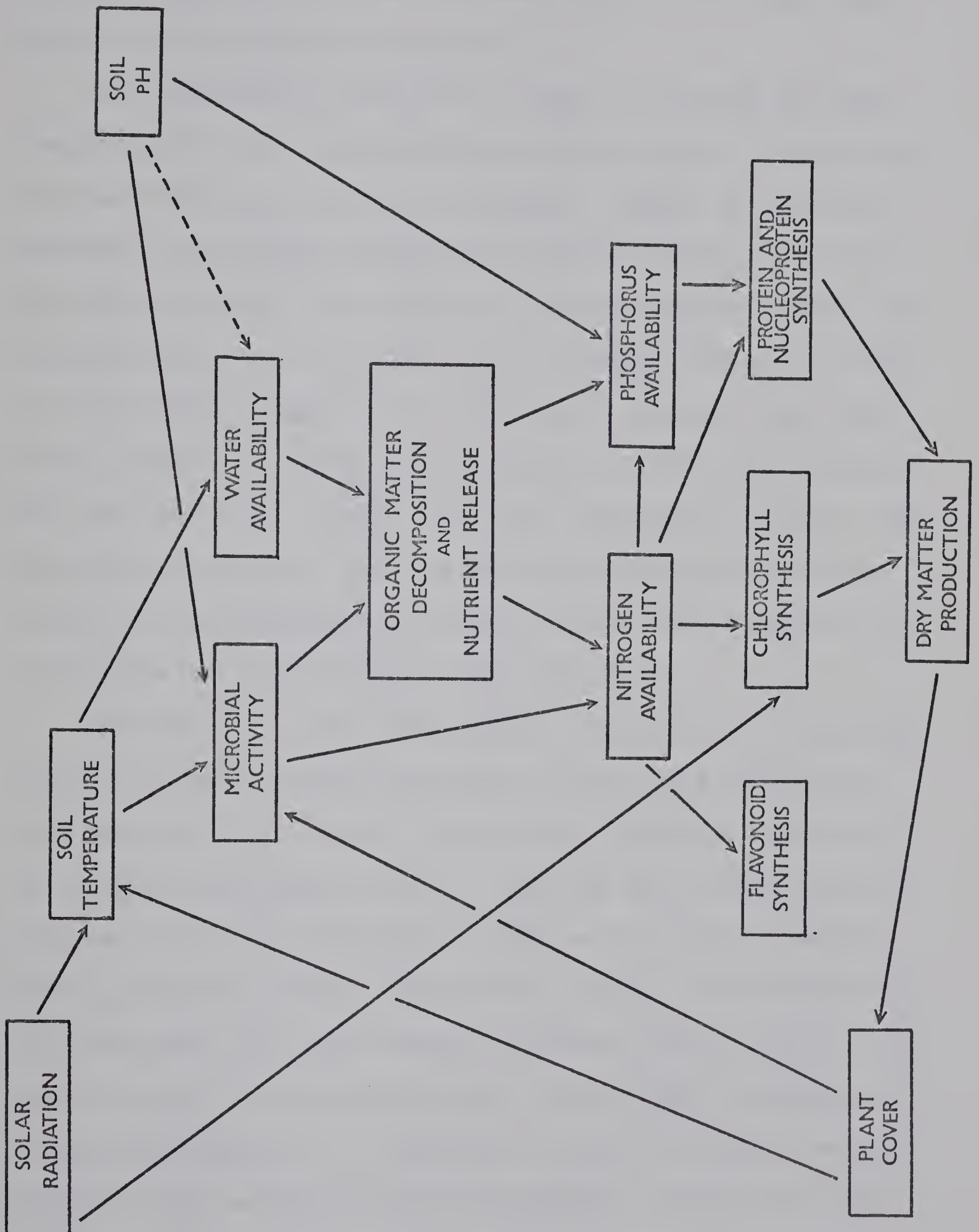
## DISCUSSION

Growth and production in both communities have been shown to be limited, relative to the genetic potential of the plants, by a low supply of available nitrogen, as demonstrated by large increases in production in nitrogen fertilized plots. Protein and nitrate analyses have shown that nitrogen metabolism by plants is not strongly limited by low soil temperatures, as had been suggested by other workers with cereal crops.

The limitation of available nitrogen supply, on the other hand, is the result of a number of environmental factors acting on the ecosystem, and thus indirectly limiting plant production in both communities (Fig. 8).

Douglas and Tedrow (1959) studied rates of organic matter decomposition in an upland tundra soil in Alaska, a soil similar to the Orthic Gleysol developed under the dwarf shrub-heath community. Decomposition rates were studied in the field by  $\text{CO}_2$  evolution, and in the laboratory in relation to varying temperature and moisture levels. They found decomposition rates to be strongly dependent on soil temperature, which is in agreement with the findings of other workers in diverse ecosystems (Witkamp 1963, 1966; Witkamp and van der Drift, 1962; Ivarson and Sowden, 1959). In the beginning of the growing season, as the active layer begins to thaw, soil temperatures averaged  $3^{\circ}\text{C}$  (Douglas and Tedrow, 1959). At this temperature,  $\text{CO}_2$  evolution from the

Figure 8. Compartment model showing the interactions between environmental factors and plant metabolism in the limitation of primary production (dashed arrow indicates uncertain influence).







organic surface layer was extremely low, and barely measurable in the mineral horizons.

As the depth of the active layer increased and soil temperatures rose, decomposition rates showed a major increase which persisted until August. Based on average decomposition rates through the growing season, Douglas and Tedrow (1959) calculated an annual organic matter decomposition rate of 0.0289 g per g organic matter (2.89%) in the upland tundra soil. This rate is much lower than those reported by Reiners and Reiners (1970) and Witkamp and van der Drift (1962) from more temperate systems. The extremely low decay rate reported by Douglas and Tedrow (1959) is undoubtedly the result of low soil temperature inhibition of microbial activity (Fig. 8).

Variation in soil temperature throughout the growing season, as well as pH, moisture content, and structural characteristics, closely approximate conditions reported by Douglas and Tedrow (1959). Thus we can regard the decomposition rates reported by them as at least a reasonable approximation for the present study. On the basis of this estimate, we can roughly calculate the amount of organic matter decomposed annually in the dwarf shrub-heath community (Table 13). Estimates of above ground standing crop are derived from the total weight (living and dead) of clipped samples from the control plots at the third harvest. The average value of  $285.1 \text{ g/m}^2$  at the end of the



Table 13. Estimated annual organic matter decomposition in two tundra communities near Tuktoyaktuk, N.W.T.

| Aboveground Stand. Crop<br>(g/m <sup>2</sup> ) | Measured Vascular Plant Production<br>(g/m <sup>2</sup> /yr) | <sup>1</sup> Estimated Total Production<br>(g/m <sup>2</sup> /yr) | Surface Litter<br>(g/m <sup>2</sup> ) | <sup>3</sup> Belowground Org. Matter<br>(g/m <sup>2</sup> ) | Total Decomposition<br>(g/m <sup>2</sup> /yr) |
|------------------------------------------------|--------------------------------------------------------------|-------------------------------------------------------------------|---------------------------------------|-------------------------------------------------------------|-----------------------------------------------|
| <u>Dwarf shrub-heath Community</u>             |                                                              |                                                                   |                                       |                                                             |                                               |
| 285.1                                          | 62.5                                                         | <sup>2</sup> 480-500                                              | 326.0                                 | 26686.1                                                     | 747.21                                        |
| <u>Wet Sedge Meadow Community</u>              |                                                              |                                                                   |                                       |                                                             |                                               |
| 195.0                                          | 72.5                                                         | 290-300                                                           | --                                    | 23010.0                                                     | 204.79                                        |

- 1

assuming root production equal to above ground vascular plant production (Dennis and Johnson, 1970) and bryophyte production equal to total vascular plant production (Bliss, 1972).
- 2

assuming 50% underestimate of above ground vascular plant production in heath-shrub community using twig clipping technique (Whittaker, 1963).
- 3

includes root standing crop (living and dead) and soil organic matter



growing season is exclusive of mosses and lichens, and agrees well with estimates of above ground standing crop from a similar community by Vikhereva-Vasilkova et al. (1964). Soil organic matter was determined from bulk density (0.35 g/cc) and loss on ignition values (74.5%) for the H horizon, with 10 cm as the average thickness of this horizon.

Calculated organic matter decay, obtained using Douglas and Tedrow's (1959) decay rate, is greatly in excess of measured total net primary production from this community ( $61.5 \text{ g/m}^2$ ). However, this estimate is probably only 50% of the true value for above ground vascular plant production (Whittaker, 1963).

Vascular plant root production estimates are variable, but an assumption of production equal to that above ground is reasonable (Whittaker, 1963; Dennis and Johnson, 1970).

Although bryophyte production data are scarce, available estimates indicate that this may equal total vascular plant production (Bliss, 1972).

The disparity between total annual production and annual organic matter decay would indicate a net annual decline in biomass in this system. However, the questionability of direct application of the estimated decay rate (Douglas and Tedrow, 1959), as well as the assumptions concerning production, do not allow such conclusions to be made.





Based on the results of soil analyses from the present study, and on estimates of organic matter chemical composition from the literature (Buckman and Brady, 1969; Paul, 1969; Waksman, 1938), the composition of this decomposed organic matter can be estimated. The values for total nitrogen determined in this study are lower than those reported in the literature. Both nitrogen and phosphorus are retranslocated by perennial plants prior to leaf abscission (Reiners and Reiners, 1970; Sutcliffe, 1962). Soil under a perennial canopy thus tends to be relatively impoverished in nitrogen and phosphorus. The preponderance of perennials in this community is in part responsible for the low nitrogen values from this soil, which represents an efficient means of conservation in a nutrient poor environment.

The annual release of nutrients in the soil can thus be determined from estimates of chemical composition and organic matter decay in this soil (Table 14). The annual release and increment of phosphorus in this soil is much lower than that of nitrogen, and thus we might expect this element to be more strongly limiting than nitrogen. The availability of phosphorus, however, is determined primarily from the rate of organic matter decomposition, the chemical composition of the soil, and pH (Fig. 8). Optimal pH for phosphorus availability ranges from 5.5 to 7.0 (Buckman and Brady, 1969). Within this range, phosphorus





Table 14. Estimated annual nutrient release from organic matter decomposition in two tundra communities near Tuktoyaktuk, N.W.T.

|                                                       | Carbon | Oxygen | Element                            |          |            |
|-------------------------------------------------------|--------|--------|------------------------------------|----------|------------|
|                                                       |        |        | Hydrogen                           | Nitrogen | Phosphorus |
|                                                       |        |        | <u>Dwarf shrub-heath Community</u> |          |            |
| % of O.M.                                             | 55.0   | 37.0   | 5.0                                | 1.0      | 0.2        |
| Annual <sub>1</sub> Release<br>(g/m <sup>2</sup> /yr) | 410.97 | 276.48 | 37.36                              | 7.17     | 1.49       |
| Annual Increment<br>(ppm)                             | 15400  | 10360  | 1399                               | 268      | 55         |
|                                                       |        |        | <u>Wet Sedge Meadow Community</u>  |          |            |
| % of O.M.                                             | 55.0   | 35.0   | 6.0                                | 2.3      | 0.2        |
| Annual <sub>2</sub> Release<br>(g/m <sup>2</sup> /yr) | 112.63 | 71.68  | 12.29                              | 4.71     | 0.41       |
| Annual Increment<br>(ppm)                             | 4894   | 3115   | 534                                | 204      | 17         |



does not tend to form insoluble complexes with other soil chemicals, and exists primarily in the monovalent state, most easily available to plants (Sutcliffe, 1962). The pH of the H horizon in the Gleysol is approximately 5.5. Some limitation on phosphorus availability may result from acid precipitation with iron and aluminum, but from the production response to phosphorus application, this is probably a minor factor.

The availability of nitrogen, on the other hand, is subject to much more complex regulation (Fig. 8). Based on the calculated annual release of soil nitrogen, the strong limitation on production seems aberrant. However, the nitrogen released through decomposition is in an organic form, and largely unavailable to most plants. The supply of inorganic nitrate, the principle form utilized by plants, is regulated by the complex series of oxidation-reduction reactions in the soil by microorganisms.

While the nitrogen cycle has received little study in arctic ecosystems, the occurrence of nitrifying and ammonifying bacteria has been reported from a range of locations (Russell, 1940; Boyd, 1958; Boyd and Boyd, 1962). Ammonifying bacteria, capable of transforming amino nitrogen to ammonium, have been reported from several tundra locations, while Boyd (1958) has determined rates of ammonification in solution under tundra conditions in a peat loam which were extremely low at soil temperatures of  $1^{\circ}$  to  $11^{\circ}\text{C}$ .



The rate of ammonification increased rapidly under higher temperatures in the laboratory (Boyd, 1958).

Nitrifying bacteria, primarily species of Azotobacter, have been reported from upland and lowland sites in both the Low and High Arctic (Russell, 1940; Boyd and Boyd, 1962). This step in the microbial transformation of nitrogen appears most strongly limited by temperature. Boyd (1958) found no evidence of in situ nitrification in an upland tundra soil, while a low rate of nitrification has been reported from dry beach ridge soils in the High Arctic (Bliss, 1972). The formation of nitrate thus appears strongly limited in the tundra, accounting for the low available nitrogen values in the control plots. Consequently, the supply is strongly limiting toward plant production.

The rate of organic matter decomposition, and the various steps involved in the transformation of nitrogen from an organic to available form, are thus strongly limited by low soil temperature, and act in combination to limit the supply of available nitrogen in the dwarf shrub-heath community (Fig. 8).

These factors likewise act to limit production in the wet sedge meadow community. However, certain additional factors unimportant in the dwarf shrub-heath also act to further limit the supply of available soil nitrogen in this community. One important consideration, mentioned earlier in relation to phosphorus, is the amount of organic matter





below the maximum depth of the active layer, and thus removed from microbial activity. While organic matter decomposition and nitrification can take place in much of the soil profile, albeit at low rates, the removal of decomposable material as the peat layer thickens represents a constant drain of potentially available nutrients from the system. This, then, must be balanced by a constant input.

Douglas and Tedrow (1959) have determined decomposition rates from a half bog soil in Alaska. Based on their site description, the wet sedge meadow appears somewhat wetter than their area; however, this is the only estimate of peat decomposition available for the Arctic to date. Decay rates, determined by Douglas and Tedrow (1959) in the same fashion as the upland heath soil, were approximately one half to one third that at the drier site (0.0089 g per g organic matter per year). The low rate of decay in the field was attributed both to low soil temperatures and high moisture levels. At low soil temperatures ( $7^{\circ}\text{C}$ ), decomposition was independent of moisture level, indicating that in the early part of the growing season, before depth of the active layer increases, the release of nutrients is extremely limited (Douglas and Tedrow, 1959). This is supported by the low nitrate content of control plants from the first harvest (Table 12). In the latter part of the growing season, as the soil warms, the rate of decomposition becomes more de-





pendent on soil moisture level (Douglas and Tedrow, 1959). We might thus expect that, as the soil dried during this period, the rate of decomposition and nutrient release will increase. This may be reflected in the higher plant nitrate values later in the growing season (Table 12). However, soil temperatures in the wet sedge meadow rarely rise above the low temperature of  $7^{\circ}\text{C}$  found by Douglas and Tedrow (1959) to limit decay rate (Fig. 7). Thus we might expect soil temperature to be the primary limiting factor of organic matter decay in this community during the growing season.

Again, on the basis of bulk density (0.27 g/cc) and loss on ignition values (84.5%) of soil samples from the wet sedge meadow, and the above estimate of organic matter decay rate in this soil, we can approximate the annual quantity of organic matter decomposition in this soil (Table 13). Again, the estimate of organic matter decomposition exceeds measured annual production ( $72.5 \text{ g/m}^2$ ). However, assuming an annual root production equal to above ground production (Dennis and Johnson, 1970), and bryophyte production equal to that of vascular plants, estimated decomposition would indicate an annual net accumulation of biomass.

The extremely low decay rate reported by Douglas and Tedrow (1959), and estimated here, is probably due to the additional limitation imposed by high moisture content in the Carex peat. Low pH of organic soils may also affect the



process, since at such values, the normal composition of the soil microbiota is altered, resulting in characteristically high populations of fungi, and low populations of bacteria (Alexander, 1961; Bliss, 1972).

Heilman (1966) stated that pH had little effect on organic matter decomposition, citing relatively recent work by Jenkinson (1965). While it is possible that pH variation has little effect on the physiology of select species, the important effect lies in changing the species composition, rather than the physiological potential of individual species.

An estimate of the annual release of nutrients from organic matter decomposition is presented in Table 14. Values for total nitrogen in the Carex peat are over twice that in the Gleysol, which may represent a lower conservation efficiency in this community than in the dwarf shrub-heath. Estimated total annual release of nitrogen is approximately 80% of that in the dwarf shrub-heath, while that of phosphorus is less than 30% (Table 14). These values are on a volume basis for a surface layer 10 cm thick, to permit direct comparison between sites (Heilman, 1966). Based on this estimate alone, we might expect phosphorus to be more strongly limiting in this community than in the dwarf shrub-heath, as seen in the response of the wet sedge meadow to nitrogen and phosphorus fertilization.



Iron and aluminum contents of Carex peat are characteristically low (Waksman, 1938), and it is unlikely that precipitation of phosphorus with iron or aluminum at low pH is significant to production. Most of the phosphorus released during decomposition probably remains available; its utilization is limited by other factors (Fig. 8).

Transformation of organic to available nitrogen in this soil is limited by the same relationships as in the Gleysol. Although Boyd (1958) and Bliss (1972) observed higher total microbial populations in peat than in mineral soils, the rate of ammonification in solution under tundra conditions in the wet soil was only half that at the up-land site (Boyd, 1958).

Nitrifying bacteria have likewise been reported from peat soils in the Arctic. Boyd (1962) reported the occurrence of Azotobacter indicus at Barrow, Alaska, but he (Boyd, 1958) failed to detect nitrification under tundra conditions. This is again primarily the effect of low temperature, although pH and moisture levels play a role as well.

The limitation on production by low levels of available nitrogen in both communities thus appears to be primarily the effect of low soil temperatures, which act to limit decay rates and transformation of organic to available nitrogen. This can also be influenced by a number of other factors. The low supply of available nitrogen influences a





number of plant processes, including protein and chlorophyll synthesis, and phosphorus metabolism (Fig. 8).

Phosphorus availability is limited primarily by the low rate of organic matter decomposition in both soils, although some precipitation with iron or aluminum may occur. Incorporation of phosphorus into organic compounds may be limited both by low soil temperature and by low available nitrogen values (Fig. 8).

Although the formation of available nitrogen is limited, the direct loss of nitrogen from the system through microbial denitrification is likewise low (Boyd, 1958). In both systems, then, the supply of nitrogen is not limiting, but rather the low cycling rate. A small amount of atmospheric nitrogen is fixed annually in both soil types (Boyd, 1958). An additional input in the dwarf shrub-heath may result from the fixation of nitrogen by symbiotic associates of Lupinus, reported by Lawrence and Hulbert (1950). Other work has indicated that this may be a widespread phenomenon among tundra plants (Lawrence et al., 1967).

In the wet sedge meadow, mats of bluegreen algae were observed on the surface during the early part of the growing season. Although no assay for fixation was made, results from similar soils in the High Arctic indicate that this may be a small input, probably not as significant as unicellular algae (Bliss, 1972).





## CONCLUSIONS

The response to fertilizer application in both communities has indicated that the supply of available nitrogen is an important limiting factor for growth and production. The supply itself, rather than nitrogen metabolism, appears to be the major limiting mechanism, as shown by both tissue analyses from the field and the results of laboratory work. Other evidence supports the widespread nature of low nitrogen as a limiting factor throughout much of the Arctic, and indicates certain characteristics which may have developed to conserve a depauperate nutrient supply.

It has been shown in this study and in other work (Miller, 1963) in nutrient deficient environments that xeromorphic characters may develop as a result of a low nitrogen regime. In the case of species from the wet sedge meadow, this xeromorphy, as shown by low protein and high fiber contents, is reversible under nutrient addition; it is a phenotypic characteristic. Many arctic species, most notable those of the Ericaceae, possess genetically determined xeromorphic characters such as thickened cuticles and thickly tomentose leaves, Ledum being a notable example. Such genetically xeromorphic species, including Vaccinium vitis-idaea ssp. minus, Ledum palustre var. decumbens, and Empetrum nigrum ssp. hermaphroditum, are both widespread and abundant in the dwarf shrub-heath community (Table 1), as



is the case throughout much of the Low Arctic (Hanson, 1951, 1953; Churchill, 1955; Britton, 1966; Savile, 1972).

Turesson (1922) and others (Waddington, 1953; Savile, 1972) have indicated that an environmental pressure may favor the development of an adaptive phenotype through a plastic response. Through time, such a pressure will lead to the development of a genotype no longer requiring the environmental stimulus to elicit that phenotype (Turesson, 1922; Savile, 1972). The existence of a genetically determined characteristic with low plasticity (xeromorphy) is evidence for a long term, widespread importance of a low nutrient regime in the development of arctic ecosystems.

A high rate of structural protein synthesis being difficult, the metabolic capacity of the plant has diverted toward the formation of structural tissues requiring little mineral input, thus making most efficient use of the photosynthetic capacity of the plant.

An efficient mechanism for conservation of nitrogen exists in the dwarf shrub-heath community. The organic H horizon is characterized by a relatively high exchange capacity (77.4 meq/ 100 g soil) and high water retentive properties. The organic layer is thus able to effectively retain both positive and negative ions in close proximity to the rooting mass, and leaching is effectively reduced. The relatively constant nutrient content of the mineral horizons in the Gleysol, even under heavy fertilizer applica-



tion, demonstrates this.

The same type of mechanism exists in the wet sedge meadow community, although on a less efficient basis. This soil is also characterized by a high exchange capacity, thus retarding the loss of positive ions including ammonium from the soil. The high moisture content in the active layer, while retaining negative ions, may so dilute the soil solution as to decrease availability to plants, as was suggested in the case of phosphorus. This may act to decrease the efficiency of nutrient utilization in this community. Cycling efficiency is further reduced by the removal of organic matter, representing a potential nutrient pool, below the active layer.

A further adaptation to the low mineral nutrient status of tundra soils may be seen in the preponderance of perennial over annual species in the arctic floras, as recently reviewed by Bliss (1971).

In perennial plants, leaf calcium and magnesium values tend to remain constant through the growing season, resulting in a large addition of these elements to the nutrient pool upon abscission. Nitrogen and phosphorus, on the other hand, tend to be retranslocated back to the stems and roots prior to leaf fall (Sutcliffe, 1962). Soils under a perennial plant cover thus tend to be relatively enriched in calcium and magnesium, and impoverished in nitrogen and phosphorus (Reiners and Reiners, 1970), as observed in both





communities. The longevity of perennial plants, as well as high root:shoot ratios (Aleksandrova, 1958; Vikhereva-Vasilkova, 1964; Dennis and Johnson, 1970) of tundra communities represent adaptations acting to conserve nutrients within the ecosystem.





LITERATURE CITED

- Aleksandrova, V.D. 1958. Measurements of above and below ground biomass of plant communities of the arctic tundra. Bot. Zhur.43:1748-1762.
- Alexander, M. 1961. Introduction to Soil Microbiology. John Wiley and Sons, New York. 472 p.
- American Society of Agronomy. 1941. Hunger Signs in Crops. Judd and Detweiler, Washington, D.C. 327 p.
- Billings, W.D. and H.A. Mooney. 1968. Ecology of arctic and alpine plants. Biol. Rev.43:481-529.
- Blackman, G.E. 1936. The influence of temperature and available nitrogen supply on the growth of pasture in the spring. J. Agric. Sci.26:620-647.
- Bliss, L.C. 1966. Plant productivity in alpine microenvironments on Mt. Washington, New Hampshire. Ecol. Monogr.36:125-155.
- Bliss, L.C. 1970. Primary production within arctic tundra ecosystems. In Productivity and Conservation in Northern Circumpolar Lands, W.A. Fuller and P.G. Kevan (eds.). IUCN Publ. New Series No. 16. pp. 77-84.
- Bliss, L.C. 1971. Arctic and alpine plant life cycles. Ann. Rev. Ecol. and Systematics 2:405-438.
- Bliss, L.C. 1972. Devon Island High Arctic ecosystem study, Summary 1971. Arctic 25:(in press).



- Boyd, W.L. 1958. Microbiological studies of arctic soils. Ecology 39:332-336.
- Boyd, W.L. 1967. Ecology and physiology of soil microorganisms in polar regions. Symp. on Pacific-Antarctic Sci. Proc. pp.265-275.
- Boyd, W.L. and J.W. Boyd. 1962. Presence of Azotobacter species in polar regions. J. Bacteriol. 83:429-430.
- Boyd, W.L. and J.W. Boyd. 1964. The presence of bacteria in permafrost of the Alaskan arctic. Can. J. Microbiol. 10:917-919.
- Britton, M.E. 1967. Vegetation of the arctic tundra. In Arctic Biology, Oregon State U. Press. pp.1-64.
- Brockman, E.R. and W.L. Boyd. 1963. Myxobacteria from soils of the Alaskan and Canadian arctic. J. Bacteriol. 86:605-606.
- Buckman, H.O. and N.C. Brady. 1969. The Nature and Properties of Soils, 7th Ed. Collier-MacMillan, Toronto. 753 p.
- Canada Department of Agriculture. 1970. The System of Soil Classification for Canada. Queen's Printer, Ottawa. 249 p.
- Chapin, T. 1971. Effect of soil temperature on phosphate uptake in cottongrass, Eriophorum vaginatum. Proc. Alaska Sci. Conf., College, Alaska. pp.25 (abstract)



- Churchill, E.D. 1955. Phytosociological and environmental characteristics of some plant communities in the Umiat region of Alaska. Ecology 36:606-627.
- Courtin, G.M. 1968. Microenvironment and energy budget of two alpine tundra communities, Mt. Washington, New Hampshire. Ph.D. dissertation, University of Illinois, Urbana. 172 p.
- Dadykin, V.P. 1958. Plant physiological research problems of the Far North. Problems of the North 1:205-216.
- Dennis, J.G. and P.L. Johnson. 1970. Shoot and rhizome-root standing crops at Barrow, Alaska. Arctic and Alpine Res. 2:253-266.
- Douglas, L.A. and J.C.F. Tedrow. 1959. Organic matter decomposition rates in arctic soils. Soil Sci. 88: 305-312.
- Duncan, D.B. 1965. Multiple range and multiple F tests. Biometrics 11:1-42.
- Eddleman, L.E., E.R. Remmenga, and R.T. Ward. 1964. An evaluation of plot methods for alpine vegetation. Bull. Torrey Bot. Club 91:439-450.
- Firbas, F. 1931. Untersuchungen über den Wasserhaushalt der Hochmoorpflanzen. Jahrb. Wiss. Bot. 74:459-696.
- Geisman, T.A. 1955. Anthocyanins, chalcones, aurones, flavones, and related water soluble plant pigments. In K. Paech and M.V. Tracey, eds. Moderne Methoden der





- Pflanzenanalyse, Vol. 3. Springer-Verlag, Berlin. pp.450-498.
- Goodman, G.T. and D.F. Perkins. 1959. Mineral uptake and retention in cottongrass (Eriophorum vaginatum L.). Nature 184:467-468.
- Gore, A.J.P. 1961a. Factors limiting plant growth in a high level blanket peat. I. Calcium and phosphate. J. Ecol.49:399-402.
- Gore, A.J.P. 1961b. Factors limiting plant growth in a high level blanket peat. II. Nitrogen and phosphorus in the first year of growth. J. Ecol.49:605-616.
- Gore, A.J.P. 1963. Factors limiting plant growth in a high level blanket peat. III. An analysis of growth of Molinia caerulea (L.) Moench. in the second year. J. Ecol.51:481-491.
- Hanson, H.C. 1951. Characteristics of some grassland, marsh, and other plant communities in western Alaska. Ecol. Monogr.21:317-378.
- Hanson, H.C. 1953. Vegetation types in northwestern Alaska and comparison with communities in other arctic regions. Ecology 34:111-140.
- Harborne, J. 1967. Comparative Biochemistry of the Flavonoids. Academic Press, London. 383 p.
- Heilman, P. 1966. Changes in distribution and availability of nitrogen with forest succession on north slopes in interior Alaska. Ecology 47:825-831.





- Hewitt, E.J., D.P. Hucklesby, and G.F. Betts. 1968. Nitrite and hydroxylamine in inorganic nitrogen metabolism with reference principally to higher plants. In Recent Aspects of Nitrogen Metabolism in Plants. Proc. Symp. Univ. Bristol, Academic Press, London. pp. 47-81.
- Hoagland, D.R. and D.I. Arnon. 1938. The water culture method for growing plants without soil. Univ. Calif. Agr. Expt. Sta. Circ. 347. Berkeley.
- Horwitz, W. (ed.). 1970. Official Methods of Analysis of the Association of Official Analytical Chemists. Assoc. Offic. Anal. Chem., Washington, D.C. 1015 pp.
- Hultén, E. 1968. Flora of Alaska and the Yukon, and Neighboring Territories. Stanford Press, Palo Alto, Calif. 1008 p.
- Ivarson, K.C. and S.F. Sowden. 1959. Decomposition of forest litters. Plant and Soil 11:237-248.
- Jenkinson, D.S. 1965. Decomposition of labelled plant material in soil. In E.G. Hallsworth and D.V. Crawford, eds. Experimental Pedology. Butterworth and Co., London. pp. 199-207.
- Jorgenson, C.A. 1927. Maglemose i grib Skov. Under sogel-  
eser over vegetationen paa en nordsjaellandsk Mose.  
Ved. Henning E. Petersen. IX. kvaelstofproblemet  
paa Maglemose og andre Hojmoser. Bot. Tidsskr. 39:  
463-487.



- Korovin, A.I., Z.F. Sycheva, and Z.A. Bystrova. 1963. The effect of soil temperature on the amounts of various forms of phosphorus in plants. Soviet Plant Physiol. 10:109-112.
- Kramer, P.J. 1934. Effects of soil temperature on the absorption of water by plants. Science 79:371-372,
- Kramer, P.J. 1940. Root resistance as a cause of decreased water absorption by plants at low temperatures. Pl. Physiol. 15:63-79.
- Kramer, P.J. 1949. Plant and Soil Water Relations. McGraw-Hill, New York. 347 p.
- Kursanov, A.L. and O.N. Kulaeva. 1957. Exchange of organic acids in pumpkin roots. Fiziol. rastenii 4:322.
- Lagerwerff, J.V. 1958. Comparable effects of adsorbed and dissolved cations on plant growth. Soil Sci. 86: 63-69.
- Lawrence, D.B. and L. Hulbert. 1950. Growth stimulation of adjacent plants by lupine and alder on recent glacier deposits in southeastern Alaska. Bull. Ecol. Soc. Am. 31:58.
- Lawrence, D.B., R.E. Schoenike, A. Quispel, and G. Bond. 1967. The role of Dryas drummondii in vegetation development following ice recession at Glacier Bay, Alaska, with special reference to its nitrogen fixation by root nodules. J. Ecol. 55:793-813.
- MacKay, J.R. 1963. The Mackenzie Delta Area, N.W.T. Dept.



Mines and Tech. Surveys, Geog. Branch, Memoir No. 8.

- Miller, M.S. 1963. Reasons for the xeromorphism of plants in high bogs. Uch. Zap. Leningr. Pedagog. Inst. im A I Gertsena 249:331-351. abstracted in Biol. Abstr. 46 (44868): 1965.
- Müller-Stoll, W.R. 1948. Der Einfluss der Ernährung auf die Xeromorphie der Hochmoorpflanzen. Planta 35: 225-261.
- Overstreet, R. and A.L. Dean. 1951. The availability of soil anions. In Truog, E., ed., Mineral Nutrition of Plants. pp.79-105.
- Pate, J.S. 1968. Physiological aspects of inorganic and intermediate nitrogen metabolism (with special reference to the legume Pisum arvense L.). In Recent Aspects of Nitrogen Metabolism in Plants. Proc. Symp. Univ. Bristol. Academic Press, London. pp. 219-240.
- Pate, J.S. and J.M. Grieg. 1964. Rhythmic fluctuations in the synthetic activities of the nodulated root of the legume. Plant and Soil 21:163-184.
- Paul, E.A. 1969. Characterization and turnover rates of soil humic constituents. Pedology and Quaternary Research. U. of Alberta, Edmonton. pp.64-76.
- Porsild, A.E. 1964. Illustrated Flora of the Canadian Arctic Archipelago. Natl. Mus. Canada Bull. No. 46.





Queen's Printer, Ottawa. 218 p.

Reiners, W.A. and N.M. Reiners. 1970. Energy and nutrient dynamics of forest floors in three Minnesota forests. J. Ecol. 58:497-519.

Russell, R.S. 1940. Physiological and ecological studies on an arctic vegetation. II. The development of vegetation in relation to nitrogen supply and soil microorganisms. J. Ecol. 28:289-309.

Saebø, Stein. 1968. The autecology of Rubus chamaemorus L. I. Phosphorus economy of Rubus chamaemorus in an ombrotrophic mire. Sci. Rept. Agr. Coll. Norway 47:1-67.

Saebø, Stein. 1969. On the mechanism behind the effect of freezing and thawing on dissolved phosphorus in Sphagnum fuscum peat. Sci. Rept. Agr. Coll. Norway 88:1-10

Saebø, Stein. 1970. The autecology of Rubus chamaemorus L. Nitrogen economy of Rubus chamaemorus in an ombrotrophic mire. Sci. Rept. Agr. Coll. Norway 49:1-36.

Savile, D.B.O. 1972. Arctic adaptations in plants. Monograph No. 6, Canada Dept. Agr, Ottawa. 81 p.

Seidenfaden, H., and T. Sorenson. 1937. The vascular plants of northeast Greenland from 74°30' to 79° North latitude, and a summary of all species found in east Greenland. Medd. om Grønland. 101:1-215.



- Shtrausberg, D.V. 1958. The assimilation of nutritive elements by plants in the polar region under various temperature conditions. *Fiziol. rastenii* 5: 226-232.
- Snedecor, G. 1957. Statistical Methods. Iowa State College Press, Ames, Iowa. 534 p.
- Sorenson, T. 1941. Temperature relations and phenology of northeast Greenland flowering plants. *Medd. om Grønl.* 125:1-305.
- Sutcliffe, J.F. Mineral Salts Absorption in Plants. Pergamon Press, London. 194 p.
- Tamm, C.O. 1954. Some observations on the nutrient turnover in a bog community dominated by Eriophorum vaginatum L. *Oikos* 5:189-194.
- Tedrow, J.C.F. and J.E. Cantlon. 1958. Concepts of soil formation and classification in arctic regions. *Arctic* 11:166-179.
- Truog, E. (ed.). 1951. Mineral Nutrition of Plants. U. of Wisconsin Press, Madison, Wisconsin. 469 p.
- Turesson, G. 1922. The genotypical response of the plant species to the habitat. *Hereditas* 3:211-350.
- Vikhereva-Vasilkova, V.V., V.A. Gavriliuk, and V.F. Shamurin. 1964. Above and below ground biomass of certain low-bush communities in the Koryak region. *Problems of the North* 8:130-147.



- Waddington, C.H. 1953. Epigenetics and evolution. S.E.B. Symp. No. 12 "Evolution":186-199.
- Wager, H.G. 1938. Growth and survival of plants in the Arctic. J. Ecol.26:390-410.
- Waksman, S.A. 1938. Humus: Origin, Chemical Composition, and Importance in Nature. Williams and Wilkins, Baltimore. 494 p.
- Warren-Wilson, J. 1954. Arctic plant growth. Adv. Sci.53: 383-388.
- Warren-Wilson, J. 1957. Some observations on the temperatures of arctic plants and their environment. J. Ecol.45:499-531.
- Warren-Wilson, J. 1959. Notes on wind and its effects in arctic-alpine vegetation. J. Ecol.47:415-425.
- Whittaker, R.H. 1963. Net production of heath balds in the Great Smoky Mountains. Ecology 44:176-182.
- Witkamp, M. 1963. Microbial populations of leaf litter in relation to environmental conditions and decomposition. Ecology 44:370-377.
- Witkamp, M. 1966. Decomposition of leaf litter in relation to environment, microfauna, and microbial respiration. Ecology 47:194-201.
- Witkamp, M. and J. van der Drift. 1963. Breakdown of forest litter in relation to environmental factors. Plant and Soil 15:295-311.



Zhurbitsky, Z.I. and D.V. Shtrausberg. 1954. The effect of temperature on the absorption of calcium and phosphorus by plants. Dokl. Akad. Nauk SSSR 96:1065-1067. abstracted in Soils and Fertilizers 17:2528.

Zhurbitsky, Z.I. and D.V. Shtrausberg. 1958. The effect of temperature on the mineral nutrition of plants. In Extermann, R.C., ed., Radioisotopes in Scientific Research, Vol. IV. Permagon Press, New York.







**B30012**